AN INVESTIGATION OF CARBON PATHWAYS IN NEW ZEALAND STREAMS

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THE STREAM TEAM

The only people who think

you can get ~~blood~~ f from a stone

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ABSTRACT

An investigation of carbon pathways in New Zealand streams was carried out using a multi-faceted, experimental approach. A series of research projects, presented as individual papers, was conducted with special emphasis on consumer processing.

Breakdown of mountain beech (*Nothofagus solandri* var. *cliffortiodes*) enclosed in coarse-mesh (3 mm) and fine-mesh (0.2 mm) bags was studied in two physically contrasting streams. Weight losses were most rapid in coarse-mesh bags held in Middle Bush Stream, a relatively stable stream with a large shredder population. The rate of leaf breakdown in coarse-mesh bags in Craigieburn Cutting Stream was similar to that in fine-mesh bags buried in both streams. Leaves in bags buried in the beds of both streams lost weight more slowly than their surface counterparts and had slightly lower protein levels and respiration rates. Larvae of the caddisfly, *Zelandopsyche ingens*, were primarily responsible for the rapid disappearance of beech leaves in Middle Bush Stream. Cage experiments demonstrated that larvae grew and survived equally well in both streams and the absence of *Z. ingens* from the Craigieburn Cutting Stream benthos was attributed to the inability of the stream to retain coarse particulate organic matter inputs. Retention appears to be the key to shredder distribution and abundance and hence is a major factor controlling litter breakdown.

The development, structure and utilisation of stone surface organic layers was investigated at two field sites in dark and natural lighting conditions. In the dark at the forest site an organic layer consisting of slime, fine particles, bacteria and fungi developed and attained maximum biomass (0.08 $mg.cm^{-2}$) in about two months. In the dark at the spring site where water was low in dissolved and particulate organic matter (DOC level <0.5 $g.m^{-3}$) no organic layer developed whereas under conditions of natural lighting at both sites, layers were dominated by diatoms and/or filamentous algae.

Laboratory experiments demonstrated the importance of dissolved organic matter (DOM) as a prerequisite for layer formation. Uptake by micro-organisms accounted for most of the reduction in levels of dissolved organic carbon (DOC) recorded in recirculating stream channels.

Radiotracer experiments (^{14}C and ^{144}Ce) showed that several common stream invertebrates could feed on "heterotrophic layers" (assimilation efficiencies 18 to 74%) and suggested that the non-autotrophic components of stone surface organic layers are likely to play a significant role in carbon transfer to the benthos, particularly in small, shaded streams.

Utilisation of allochthonous and autochthonous inputs by benthic invertebrates was investigated using stable carbon isotope analysis. The faunas of small, forested streams depended primarily on allochthonous sources of carbon whereas variable utilisation of allochthonous and autochthonous materials was shown by species from a grassland stream. Relatively depleted ^{13}C values obtained for the mayfly *Deleatidium* taken from forested sites suggest that its larvae assimilate algae selectively. A shift to greater dependence on autochthonous energy sources was shown by invertebrates from small recently clear-cut catchments (1-4 years) in response to canopy removal and flushing of forest-derived organic materials. Although only of a preliminary nature, my results suggest that stable carbon isotope analysis is a useful technique for providing insights into trophic linkages within stream communities.

Finally, the influence of physical factors and forest type on the distribution of benthic invertebrate faunas in 43 New Zealand streams was investigated using a systematised survey technique. Several common taxa were numerically dominant at most sites regardless of forest type and both distribution of shredders and faunal diversity were related to stream stability. Implications of these findings for forest-stream management are discussed.

In general, New Zealand stream ecosystems are viewed as being strongly dominated by physical factors which determine and limit the framework within which biological communities can function. Integration of the mass-balance and intra-system approaches to carbon processing is suggested as the logical way to promote understanding of carbon flows to, from and within stream ecosystems.

CHAPTER I

GENERAL INTRODUCTION

The purpose of this Introduction is to provide the reader with background material pertinent to this thesis. I propose to do this by discussing relevant literature and by bringing the reader up to date with a thorough review. I will then outline the research questions dealt with and explain the rationale and approach used in the research and in the presentation of results.

Roots of Ecosystem Ecology

The broad field of what is known today as ecology can trace its roots to several different groups of early, independent scientists who developed what are now particular aspects of modern ecology. For example, early naturalists such as Audubon & Brewster, in the early 1800's, developed the roots of today's autecology work which includes the study of life histories and behaviour. Malthus' early work, late 1700's, on population-food supply relationships initiated population ecology which later was expanded to encompass mathematical elements, e.g., Lotka's work in the 1920's.

Studies on plant distribution by early plant geographers, Humboldt, Gray and Kerner in the mid to late 1800's laid the foundation for community ecology. Later, in the early 1900's, Cowles, Clements and Tansley defined the structure, composition and dynamics of whole plant communities, while in the United States and England, Shelford (1911) and Elton (1927), respectively, considered plants and animals as components which together comprise a community. The search for general principles governing the organisation of communities dates from this period. Two principal and opposing viewpoints on the "nature" of the biological community emerged. On the one hand, the community was viewed as an organism composed of interdependent units (species in a community like organs and tissues in an individual) functioning together as mutually interdependent elements of a larger clearly defined whole. This organismic concept was put forward initially by Clements (1916) and grew out of parallels he recognised between ecological succession (community development) and the developmental stages of an individual organism. On the other hand, Gleason's (1926) individualistic concept envisioned a community as a collection of species that simply happened to exist together through converging accidents of space, time and similar environmental needs. Gleason's concept, developed after that of Clements', was conceived

initially as a result of his studies of flood-plain forests in the Mississippi valley where community components appeared together as a "conglomeration of interchangeable parts" (Richardson, 1980).

The concept of the ecosystem grew out of these community concepts. While Tansley (1935) was the first to clearly coin and define the term ecosystem, the idea had appeared as early as 1887 in Forbes' paper "The Lake as a Microcosm". While disagreement as to the nature of the relationships between species in an ecosystem still exists, the ecosystem concept has provided a convenient basis for many scientific studies.

The work of Thienemann, Hutchinson (1900 - 1940) and particularly Lindeman (1942) did much to foster the ecosystem concept and led to the development of modern ecosystem ecology. Since Lindeman's time, ecologists have worked at one of four levels - the individual organism, the ecosystem, the single species population or the community level (Macfadyen, 1975) which remain the principal foci today.

In a bold attempt to understand the fundamental principles underlying the structure and functioning of ecosystems, Lindeman (1942) clearly perceived that energy and nutrients are common requirements of all organisms as indicated by the following quotation (Lindeman, 1942): "Although certain aspects of food relations have been known for centuries, many processes within ecosystems are still incompletely understood. The basic process in trophic dynamics is the transfer of energy from one part of the ecosystem to another."

In what is still an appealing concept he perceived that studies of ecosystem dynamics and interactions yield important information not obtainable by studying just their biological components. He grouped taxonomically different species together into trophic levels thereby permitting analysis not confined by the rigors of taxonomy. Such a functional approach, sometimes utilising other functional groups, e.g., functional feeding groups as in stream ecosystems (Cummins, 1974; Hawkins & Sedell, 1981), has been followed in numerous subsequent studies and has been of particular value in management studies (Reichle, 1975).

While it is easy to criticise Lindeman's work today, e.g., his simplified assumption of trophic levels (Darnell, 1961) and his calculation of efficiencies which have been misused by ecologists for many years (see Warren, 1971 for discussion), I believe that time has

shown the value of his approach to problem-solving in ecological research. Ivlev (1945), in a thoughtful discussion, while not accepting the concept of trophic levels with "all its endearing simplicity", agreed with Lindeman on the necessity of an ecosystem approach and the value of dealing in dynamic and energetic terms.

From the 1940's ecosystem ecology "took off" and at this juncture I will outline the development of the ecosystem approach in running waters as it relates to my own research.

Ecosystem Ecology and Its Development in Running Waters Research

One of the first aspects of stream ecosystem research to be developed was concerned with determining the metabolism of stream communities by calculating energy inputs in terms of carbon fixation rates. H.T. Odum (1956), in an important paper, argued for and presented a method for determining gross primary production as the amount of carbon fixed as a result of photosynthesis in a particular stream reach. By monitoring the oxygen content of the water entering and leaving a particular stream segment, either continuously or at frequent intervals, Odum worked out the weight of carbon fixed per unit area in a number of streams. One of the main weaknesses of the method is the need to accurately estimate diffusion, i.e., the rate of uptake from, or loss to, the atmosphere (see Owens, 1965 for a discussion of problems encountered in attempting to estimate diffusion). This is a major problem in swift, shallow, turbulent streams where diffusion from the air tends to maintain dissolved gas concentrations at close to saturation levels at all times.

Despite this problem, Odum's methodology served as a starting point for workers to estimate parameters of ecosystem metabolism. Odum's classic work on Silver Springs (1957) was followed by a rash of studies which attempted to evaluate accurately the input of energy to an ecosystem, its transfer between trophic levels and the corresponding energetic efficiency of the community. Teal's work (1957) on energy flow through a spring ecosystem was highly successful, probably because the system he chose to work on was so small (2 m wide). Although the delineation of trophic level energy transfer is a difficult task to accomplish, this type of work continued and, as a result, numerous workers have devised or borrowed methodologies from other disciplines (e.g., physics, chemistry, medicine) to estimate energetic parameters at the individual ecosystem level, e.g., radioisotopes, calorimetry, etc.

With Tilly's work (1968) on a small spring, a study which considered the community in terms of trophic levels and species populations, came attempts to relate ecosystem energy flow characteristics to the "unifying principles" proposed by Margalef (1960, 1963, and later in 1968). Margalef suggested that evolution in communities led to stabilisation of the structure and function of an ecosystem and therefore the maturity of an ecosystem could be measured in terms of observable structural and metabolic relationships. Tilly (1968) considered Cone Spring as an ecosystem "maintained in immaturity by the deformational influence of flow, the restrictions of small size and the limits placed upon reproduction by low temperature". Subsequently, Hall (1972) detailed animal migration in a stream ecosystem by considering what percentage of an ecosystem's energy budget was tied up in a migratory portion. He measured seasonal patterns of stream metabolism and fish migration and considered his results in relation to Margalef's (1963, 1968) proposals on migration and its role in determining ecosystem maturity.

Probably one of the most influential and important studies on energy flow in running waters was that of Fisher & Likens' (1972, 1973) on Bear Brook, New Hampshire, U.S.A. Using a mass-balance approach they constructed an organic energy budget for Bear Brook, a small, forested, first-order stream. They delineated the potential vectors for energy input to and output from the stream and measured the quantity of material passing by way of them. By detailing the different energy input and output vectors they enabled comparisons of organic energy budget components to be made with those of other streams (e.g., Sedell *et al.*, 1974; McCammon, 1978). Further, while aquatic biologists previously had suggested that the benthic faunas of streams were largely dependent on allochthonous inputs for food (e.g., Nelson & Scott, 1962; Hynes, 1963, 1970; Minshall, 1967), Fisher & Likens demonstrated the importance of allochthonous inputs as an energy source to the stream community *in general*. Their work clearly demonstrated that Bear Brook and potentially many other streams are processors of organic materials (see also Fisher, 1977), a concept which has been refined and extended and has led to a whole gamut of research which I will discuss below.

Intra-System Dynamics: Stream Processes

While the mass-balance studies of Fisher & Likens (1972, 1973) and others (e.g., Sedell *et al.*, 1974; Fisher, 1977; Mulholland, 1981a)

have elucidated the organic matter processing characteristics of streams, they intentionally avoid examining the individual processes which occur within the stream ecosystem; the "nitty-gritty of carbon utilisation". Intra-system work has been spearheaded by K.W. Cummins and an overview is provided in his paper, "Structure and function of stream ecosystems" (Cummins, 1974). In his earlier work in Pennsylvania, e.g., Cummins *et al.* (1966), he attempted to detail food webs in natural invertebrate communities; a difficult task to say the least. After dissecting what must have been thousands of insect guts, Cummins (1973, 1974) suggested that stream ecosystem research might make more progress by avoiding taxonomic barriers which are so prevalent in stream work when working with immature aquatic larvae and considering the species as the basic taxonomic unit. He proposed viewing lotic invertebrates from a functional standpoint; animals being categorised functionally according to size of particles ingested and by other characteristics of their food and feeding modes. Cummins' functional approach coupled with data obtained via Fisher & Likens' (1973) mass-balance approach, offered the opportunity to stream ecologists to begin to identify process-related questions and to examine, both quantitatively and qualitatively, the functional groups involved and their effects on these processes. In some cases it has aided in the development of management strategies for watercourses, a result hoped for by Cummins (1974).

It is within the realm of process-related research that my work falls. Therefore, I will outline in some depth relevant work of this kind carried out to date both overseas and in New Zealand.

Processing of Allochthonous Inputs in Forested Streams

The demonstration by Fisher & Likens that small woodland stream communities were dependent on allochthonous materials for their primary source of energy served to strengthen and complement the findings that many aquatic insects ingest and presumably depended on large quantities of forest detritus as food (e.g., Hynes, 1963; Minshall, 1967). Kaushik & Hynes (1968, 1971) and Mathews & Kowalczewski (1969) were among the first aquatic workers to employ the litter bag method, previously used in terrestrial decomposition studies (e.g., Edwards & Heath, 1963; Witkamp & Olson, 1963; Witkamp & Crossley, 1966), to simulate natural leaf aggregations in leaf decomposition studies in streams. Leaf bags and unenclosed leaf packs (Reice, 1974, 1977, 1978; Petersen & Cummins, 1974; see Cummins *et al.*, 1980 for a comparison of the two methods) subsequently have been

used on numerous occasions to estimate decomposition rates. The results of this work can be divided into two parts. The first has been to increase our understanding of the role of micro-organisms, particularly bacteria and aquatic hyphomycete fungi in the breakdown of leaf litter (Bärlocher & Kendrick, 1974; Suberkropp & Klug, 1974). Second, attention has been focused on the relationships between microbially colonised or "conditioned" detritus (Cummins, 1974) and large particle detritivores or shredders. Cummins (1974) presented his now famous "peanut butter and crackers" analogy where high quality (low C:N ratio) microbial tissue was considered analogous to protein rich peanut butter which occurs only on low quality (high C:N ratio) crackers, the terrestrial leaf material. Considerable work has accumulated which suggests that shredders do indeed depend largely on the microbial component of decomposing litter for nutrition (e.g., Kaushik, 1969; Wallace *et al.*, 1970; Bärlocher & Kendrick, 1973a, b). However, Iversen (1974) and Baker & Bradnam (1976) calculated that microbial biomass could account for only a small fraction of the nitrogen and energy intake of detritivores they examined and concluded that non-living detritus must represent their main food source. Winterbourn (1982) demonstrated that larvae of the shredding caddisfly *Zelandopsyche ingens* assimilated some of the lipid and digestible carbohydrate components of detritus with high efficiencies, 43 and 26% respectively, implicating higher plant detritus as an important carbon source.

In the early to mid 1970's, considerable stream work focused on the processing of large particle detritus (see Boling *et al.*, 1975) and as numerous stream ecologists had entomological training the interaction between detritus and shredders became a focal point of their research. Numerous feeding studies have demonstrated the preference of shredders for detritus with the highest rate of decay or the most microbially conditioned leaves (e.g., Wallace *et al.*, 1970; Kaushik & Hynes, 1971) while growth studies with shredders, both in the laboratory (e.g., Anderson & Grafius, 1975) and the field (Otto, 1974; Grafus & Anderson, 1979), have directed attention to the differences in food quality and breakdown rate of different aged detritus of the same and different leaf species (Petersen & Cummins, 1974).

This shredder-microbe-detritus linkage has become incorporated as a central theme in models and concepts of stream processes. Cummins *et al.* (1973) used a mass-balance approach with various shredders and

collectors in a laboratory stream to quantify their role in the breakdown and disappearance of CPOM (coarse particulate organic matter) and calculated that shredders accounted for *ca.* 19% of CPOM breakdown. On this basis they calculated that populations of two species of *Tipula* and three species of *Pycnopsyche* could be expected to process at least half of the estimated CPOM inputs to a Michigan stream. McDiffett (1970) also estimated shredder impact on litter breakdown and gravimetrically determined that *Pteronarcys scotti*, a shredding stonefly, fragments about 4.5 g dry wt of leaf material per larva per year. Winterbourn & Davis (1976) (in a New Zealand study, discussed in more detail later) estimated that *Zelandopsyche ingens*, a large shredding caddisfly, could process up to 16% of the annual leaf inputs to a small mountain beech stream in New Zealand.

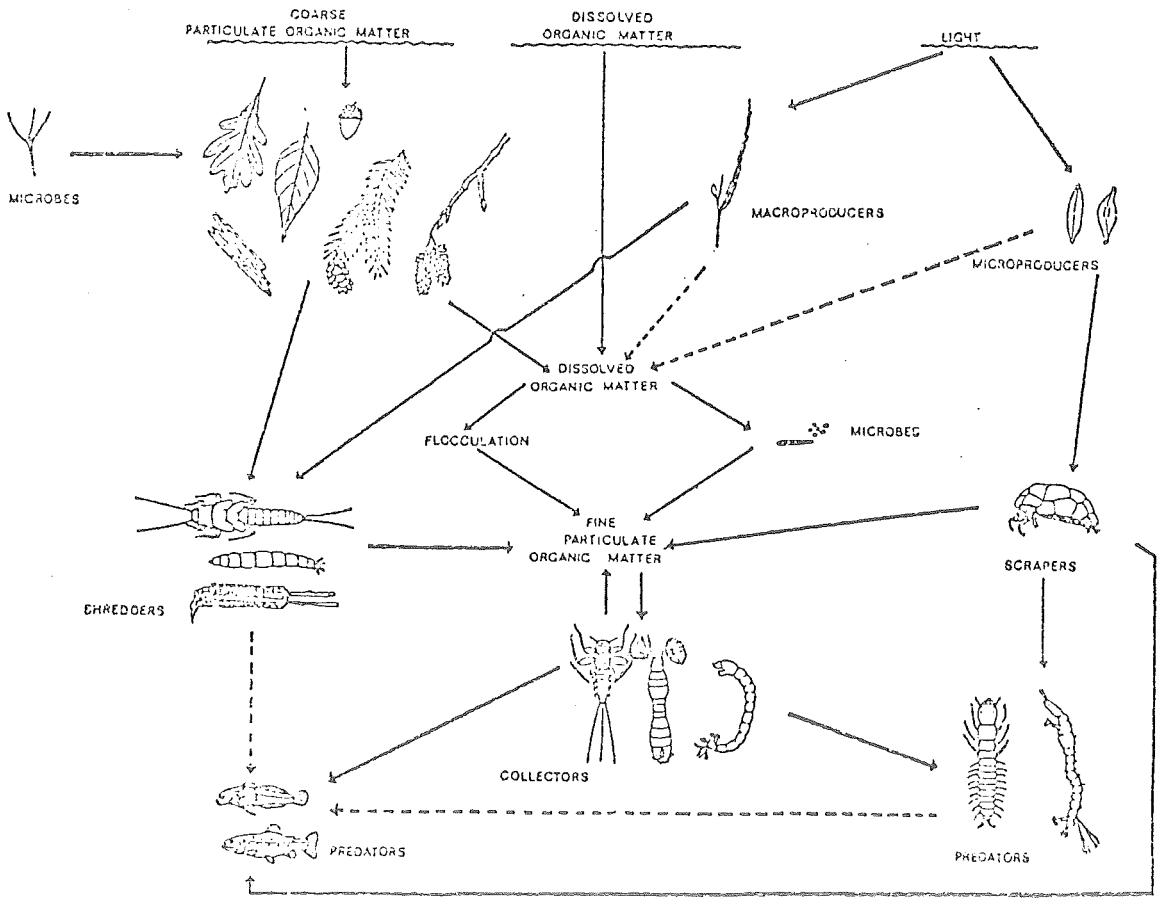
These and related studies on breakdown activity of shredders, coupled with measurements of allochthonous inputs, have led to the development of a conceptual framework of feeding relationships in forested stream systems which emphasise the importance of shredders as the initial processors of microbially colonised CPOM. Processed inputs enter the fine particulate pool as FPOM (fine particulate organic matter, >0.45 µm, <1 mm) and serve as food for collector insects (Cummins, 1974). Cummins (1971) states, "Once the leaves are conditioned by microbial colonisation, the large detritivores or 'shredders' begin the process of leaf fragmentation leading to the development of consumer populations which feed upon smaller particles, the 'collectors'. Although microbial activity is sufficient to eventually breakdown the terrestrial inputs, shredder densities and feeding rates are usually sufficient to reduce the majority of the litter to smaller particles - shredder feces and fragments resulting from the feeding process."

It is this concept of shredders causing particle size reduction which still underlies much lotic feeding relationships work. A series of papers all incorporating the previously discussed estimates of shredder impact have led to statements like that of Hynes (1975) that shredder feeding lies "at the base of almost all the biotic activity in the water". This is seen again in Grafius & Anderson (1979) - "The major role of *Lepidistoma quercina* [a shredding caddisfly] is not as a direct source of insect biomass.... However, the feces produced by *L. quercina* are a highly significant contribution to the food chains of simuliids and other collector species. No data are available on the utilisation of insect feces by simuliids. However, because fecal material can theoretically be recycled through the collectors a number

of times until all of it has been assimilated....". In similar vein, Short & Maslin (1977) concluded that "shredders are of great importance ... with regard to nutrient availability to various collector species".

This view of a stream ecosystem as having strong linkages between forest vegetation-microbes-shredders-collectors had become the major paradigm of lotic theory at the beginning of my thesis research. Emphasis on detrital forest inputs and their processing by shredders in small, temperate, forested streams was common.

To summarise, Northern Hemisphere researchers, particularly those in North America, have emphasised the input and colonisation of forest-derived organic material (allochthonous inputs) and subsequent reduction in particle size as a result of feeding by large particle detritivores. These smaller particles enter the fine particulate pool and then serve as a food source for invertebrates both locally and downstream. While other mechanisms for FPOM generation have been discussed (e.g., Anderson & Sedell, 1979) and in a few cases examined (e.g., Lush & Hynes, 1973) the bulk of the literature still implicates the shredder pathway as the primary linkage to the invertebrate community. This paradigm is clearly illustrated by Cummins (1974) in the following figure from his work.



DOM in Stream Ecosystems

Before I complete this portion of the review I will discuss what may be the most important, yet least known organic carbon component of stream ecosystems, dissolved organic matter (DOM). (The carbon component of DOM is known as DOC [dissolved organic carbon].)* While representing the largest reduced carbon pool in streams (Hobbie & Likens, 1973; Moeller *et al.*, 1979) DOC remains poorly known from both a structural and functional viewpoint (see Dahm, 1981 for a review). Information on the transfer of DOM to the particulate pool and up the food chain is sparse. Little is known about how stream ecosystems deal with DOM except to say that they must process it since they do not overload (McDowell & Fisher, 1976).

Carbon budget work for small streams in the north-eastern United States indicates that DOM represents 79-88% of carbon exported (Hobbie & Likens, 1973). Wetzel & Manny (1977) showed that 75% of the carbon in transport in Augusta Creek, Michigan was DOC.

Sources of DOM are many and include soil exudates, leaf leachates, macrophytic and algal material, invertebrate excretions, bacterial slimes and decomposing, terrestrial vegetation. The relative contributions of these inputs appear to vary between seasons and environments (Dahm, 1981). In a DOM budget for a small deciduous forested stream in Massachusetts, McDowell & Fisher (1976) estimated that 42% of the total autumnal DOM input was derived from leaf litter which had entered the stream. Klotz & Matson (1978) suggested that larger rivers would have a more quantitatively and qualitatively heterogeneous DOM pool as a result of the greater combination of potential sources contributing to the system.

The chemical composition of DOM remains poorly resolved. Several attempts have been made to characterise it (Larsen, 1978, Wallis *et al.*, 1981), but because of its heterogeneous nature and the lack of biochemists working on the problem, its composition remains an enigma. However, some things are known about its components. Nykvist (1963) in an early, somewhat ignored, yet important piece of work, prepared extracts of

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* Reference in the literature to organic material as being "dissolved" or soluble refers to substances that passed through a 0.45 µm filter. Lock & Hynes (1975) point out this "is only a convenient and reproducible cut-off point along a spectrum of particle size and it is important to remember that the 'dissolved' fraction may include colloids as well as material in true solution".

different leaf species, performed qualitative chemical assays of the resulting leachates and determined that aliphatic acids, amino acids and sugars were present in large amounts (up to 25% in the leachate). However, he was unable to identify the remainder. Fifteen years later, Larsen (1968) had similar difficulty. Twenty percent of the DOM from a small Pennsylvania river could be identified as carbohydrate, phenol, protein or amino acids and he considered the remainder was probably fulvic-acid like material. Wallis *et al.* (1981) found that as a rule only about 40% of the total dissolved organic load in Marmot Basin, Canada could be identified. In general, DOM consists of what appears to be grossly similar to the familiar, but poorly characterised, "humic" or fulvic-acid fractions known from soil. These fractions consist of an amorphous mixture of highly oxygenated polymeric molecules (Larsen, 1978).

Studies involving DOM utilisation have been of a rather cursory yet stimulatory nature. Nykvist's (1963) early fundamental work on leaching and decomposition of leaf leachates demonstrated that the characterisable components of leachate rapidly disappeared during leachate decomposition, with uptake being more rapid in aerobic than anaerobic conditions. Wetzel & Manny (1972a) and Cummins *et al.* (1972) monitored a series of biological and chemical variables in a laboratory stream following the introduction of hickory (*Carya glabra*) and maple (*Acer saccharinum*) leaves. In contrast to later work, their studies demonstrated that DOM processing was primarily by bacteria in transport rather than by microbes inhabiting benthic substrates. Their results demonstrated the rapidity and thoroughness with which "natural" streams process natural leachate, except for some resistant organic carbon and nitrogen compounds. This is in agreement with Manny's (1972) work which demonstrated rapid decomposition of DOM and DON (dissolved organic nitrogen) in a hard water stream where only highly refractory components of DON remained in the stream water "at any distance from its source". Lock & Hynes (1975, 1976) studied the disappearance of leaf leachates of sugar maple (*Tsuga occidentalis*) and red pine (*Pinus resinosa*) under laboratory conditions using small recirculating bowls with or without stream-bed sediment in both sterile and non-sterile conditions. In contrast to Cummins *et al.* (1972) and Wetzel & Manny (1972a) who attributed leaf leachate disappearance to bacteria in the water column, they found (Lock & Hynes, 1976) that water column reduction of DOC was never greater than 20% of the original concentration after four days. However, in experiments with biologically active stream bed sediments placed in the experimental bowls they found

almost total leachate removal in two days, i.e., a reduction in DOC levels to pre-experimental "background levels". While cautioning the validity of drawing broad conclusions from their artificial experimental set-up they suggested that their results "fit in well with the concept of the organic layer around stones (Madsen, 1972). It seems that one site of microbial uptake is the matrix of bacteria, extracellular materials, fungi and organic and inorganic particles surrounding all surfaces in streams". They went on to say that the organic layer could represent an important food resource for the grazers and detritivores of the benthos, a point which will be considered further in this thesis.

In an attempt to determine the relative importance of biotic and abiotic pathways for removal of DOM from water, Dahm (1981) used recirculating chambers and radioactive alder (*Alnus rubra*) leachate. He found microbial uptake of DOM to be kinetically slower than abiotic, adsorptive uptake. However, microbial uptake was much more effective in the removal and degradation of the *total* DOC pool. In 48 hours, 97% of ^{14}C-labelled leachate disappeared from solution by adsorption ($\simeq$ 20%) and microbial uptake ($\simeq$ 77%). In contrast, Lush & Hynes (1973) demonstrated that abiotic reactions affected by pH, water chemistry and leaf species could cause decreases in DOC levels of up to 50% of the initial level in 60 hours. As stated by Dahm (1981) the capacity for abiotic DOM uptake is a complex one to determine and each process might be expected to vary in efficiency depending on a large number of environmental factors.

One possible explanation for the variation in estimates of DOC uptake rates and mechanisms (abiotic vs biotic) is clear from Dahm's work (1981). Certain components of DOM appear to be more biologically utilisable or labile than others (which are termed refractory). Numerous workers since Nykvist (1963) have pointed out the existence of refractory organic carbon which is particularly resistant to microbial uptake. Further, McDowell & Fisher (1976) contended that a considerable fraction of DOM released by initial leaf leaching was highly labile and readily utilised by stream microbes. McDowell & Fisher (1976) suggested that highly labile compounds were released by forest floor litter as well and were probably utilised by the microbial community in the forest soil. Therefore, DOM entering the stream as ground water which has been "picked over" by terrestrial microbes is likely to be largely refractory and of minor significance to lotic food webs (Dahm, 1981). In support of this contention, Wetzel & Manny (1972b) found that the ratio of labile

to refractory DOM increased, and the C:N ratio decreased, at the point where a Michigan stream expanded and flowed slowly through a productive marsh from which it received extensive drainage. In addition, Wallis *et al.* (1979) found that DOM in stream water from Marmot Basin, Canada, a subalpine forest region, had carbon 13/12 ratios indicative of having been "well worked over and refractory in nature". However, at one site (a 150 m tributary with short water residence time, 30 minutes) where overland seepages occurred and "short-circuiting" (in terms of McDowell & Fisher, 1976) of the terrestrial microbes was possible, carbon 13/12 ratios were lower suggesting that labile components (lighter 13/12 components) had not been respired away completely.

Despite the constructive nature of research to date, DOM dynamics in streams are not well understood and require much further attention.

New Zealand Stream Work and the Development of Stream Ecology

In order to further clarify the background to my work I will briefly review past running water studies in New Zealand with particular reference to recent work and its place in stream ecosystem research internationally.

Much of the stream biology research in New Zealand has been of a taxonomic nature until recently. Generally, each major aquatic invertebrate order has had both past and current workers continually describing and then revising the fauna at many taxonomic levels, e.g., Ephemeroptera: Phillips (1930), Towns & Peters (1979); Plecoptera: McLellan (1977), Winterbourn (1964); Trichoptera: Cowley (1978), McFarlane (1951); Mollusca: Winterbourn (1970); Crustacea: Hopkins (1970). General introductory accounts of the fauna have been written by Marples (1962) and Pendergrast & Cowley (1966) and comprehensive keys to the local insect fauna are given by Winterbourn & Gregson (1981).

Life history studies of benthic invertebrates have a relatively long history in this country (e.g., Hamilton, 1940; Michaelis, 1973; Towns, 1981, see references therein) and more recently drift of aquatic insects has received local attention (McLay, 1968; Watson, 1971; Cadwallader, 1975).

Besides being of local interest, New Zealand stream faunas are of interest to biologists elsewhere because of their degree of endemism and southern affinities. Therefore, several workers have been concerned with the biogeography of the New Zealand representatives of particular

insect orders or families in relation to their world distribution (e.g., Trichoptera: Ross (1967); Ephemeroptera: Edmunds (1975); Plecoptera: Illies (1965); Chironomidae: Brundin (1966)). The most recent discussion of the New Zealand fauna and its biogeographical affinities is that of Winterbourn (1980, see references therein for further details).

In addition to taxonomic work, freshwater fisheries research has a long history in New Zealand with Hutton's work in the mid to late 1800's serving as a starting point (see McDowall (1978) for a review). Allen's (1951) classical study on the Horokiwi Stream while he was a Research Officer with the Freshwater Section of the Marine Department is well known. His work on the trout and benthos of the Horokiwi Stream represented one of the first attempts to obtain data on trout population dynamics and develop techniques useful in this pursuit. His approach to the work was clearly influenced by Lindeman (1941) and Macfadyen (1948), and is a good example of Ivlev's (1945) "product of interest" type of research.

After Horikiwi, Allen produced several smaller yet valuable publications on the distribution of New Zealand benthic faunas. His 1956 and 1959 papers were particularly concerned with physical habitat structure and the control it exerts on the nature of the bottom fauna. In what now appears to be a timely conclusion, Allen (1960) commented, from a minimal data base, that removal of original, native forest cover in New Zealand and its replacement by pasture had comparatively little effect on the bottom fauna of streams. Other fisheries work has included work on the production,behaviour and general biology of various species (e.g., Benzie, 1968; Cadwallader, 1973; Staples, 1975) and competition between different species of native and introduced fish, particularly trout (e.g., Hopkins, 1965; see McDowall, 1978 for more details).

The effects of pollution on New Zealand stream communities has received considerable attention in the past and single stream studies are numerous (e.g., Cameron, 1970 and Toshach, 1977 in the South Island; Stone, 1965 and Gibbs & Penny, 1973 in the North Island). In a broader context, Winterbourn (1981) discussed the use of benthic invertebrate community analysis as a water quality assessment tool.

In related water quality work, scientists at Freshwater Section, Ecology Division, D.S.I.R. have, in the last ten years, concerned themselves with nutrient dynamics. Work in experimental catchments, the Taita and Puketurua, near Wellington and Whangarei respectively, has

dealt with nutrient run-off in basins with different terrestrial vegetation (White, 1972; McColl *et al.*, 1975, 1977); complementary work by McColl (1974) considered the uptake of stream nutrients by sediments of small streams under varying nutrient regimes. Lock & John (1979), using ^{32}P in a laboratory stream, examined the effect of flow patterns on phosphorous uptake by river periphyton under biotic and abiotic conditions. Additionally, White & Downes (1977) determined catchment sources of phosphorus and nitrogen to Lake Taupo in order to improve assessments of lake nutrient status by detailing nutrient loading from the surrounding catchment.

The effects of logging on stream communities, which has been studied extensively overseas, has received limited attention to date in New Zealand (Graynoth, 1979; see Cowie, 1980 for a review). The only direct study of logging effects was carried out by Graynoth (1979) in the north-west Nelson area. However, research modelled after the ecosystem work pioneered at the Hubbard Brook Experimental Forest (see Likens *et al.*, 1977) is being carried out primarily in the New Zealand Forest Service experimental catchments at Maimai and Big Bush and is contributing substantially to our knowledge of hydrology as well as nutrient and sediment dynamics following deforestation of West Coast streams (e.g., Neary *et al.*, 1978; O'Loughlin *et al.*, 1980; Mosely & Rowe, 1981).

The ecosystem approach to streams had not been used in New Zealand prior to the 1970's and its development owes much to the work of Dr M.J. Winterbourn and his students at Canterbury University in Christchurch. His early work on taxonomy and life histories of the New Zealand Plecoptera (1965, 1966) was performed at Auckland University which has been a centre for much freshwater insect research (Tan, 1961; Norrie, 1969; Towns, 1979). After later work on molluscs (1970) and some ecologically influenced caddisfly life history work performed with an IBP research group in Canada (1971a, b) Winterbourn began stream process-oriented research influenced by North American workers such as Cummins (1973, 1974). He argued that trophic relations of benthic invertebrates were a key to understanding energy flow and community dynamics which were being emphasised concurrently in North America. Initially, he and his students examined the dynamics of predacious insects and prey in several New Zealand rivers (Winterbourn, 1974; 1978a; Devonport & Winterbourn, 1976).

Later, to complement Northern Hemisphere research (e.g., Fisher & Likens, 1972, 1973; Iversen, 1973; Hynes *et al.*, 1974), he began a series

of experiments on the input and processing of detritus at Middle Bush Stream, a mountain beech forest stream located at Cass, Canterbury in 1973. A series of publications, conference presentations and ideas have resulted from this work and served as the basis for my research into New Zealand stream processes. This work includes an annual energy budget for particulate organic matter (Winterbourn, 1976), later complemented by the construction of a complete carbon budget (both particulate and dissolved) of the Fisher & Likens' (1973) type (McCammon, 1978). Specific work on the role of the oeconesid caddisfly *Zelandopsyche ingens*, an important shredder found in Middle Bush Stream, included field and laboratory studies into aspects of its life history, larval ecology and feeding (Winterbourn & Davis, 1976). A more complete examination of the fauna of Middle Bush Stream (Winterbourn, 1978b) emphasised life history and seasonal changes in insect abundance and colonisation behaviour. Leaf processing work and the role of micro-organisms in litter breakdown was also conducted using leaf bag techniques (Davis & Winterbourn, 1977; Winterbourn, 1978c).

The results of this work, while influenced by the North American approach, have yielded some interesting deviations from North American findings. In a significant discussion, Winterbourn (1976) outlined some of the "quirks" of New Zealand streams which make them unique in comparison to the well known temperate forested streams of North America. Winterbourn (1976) observed that, unlike North American streams where "a significant portion of this energy (allochthonous inputs) enters the aquatic food web through the feeding activities of large particle detritivores which break down leaves into smaller fragments that can be ingested by grazing and filter feeding invertebrates (Petersen & Cummins, 1974)", large particle detritivores are not abundant in New Zealand. *Zelandopsyche ingens* and other leaf-feeding species of Oeconesidae (Trichoptera) are uncommon, and although larvae of the large detritivorous stonefly *Austroperla cyrene* are widely distributed, they are rarely abundant. Winterbourn (1976) noted that the Northern Hemisphere trichopteran families Limnephilidae and Lepidostomatidae, whose larvae are important shredders (Cummins, 1974), as well as the plecopteran families Pternonarcidae and Peltoperlidae, which also contain shredders, do not occur in New Zealand.

Even in Middle Bush Stream, which has an unusually large population of *Z. ingens* (50-100 larvae.m^{-2} Winterbourn & Davis (1976) estimated that these caddis fragment only 6-12% of the annual input of beech litter. Although probably a high value for a New Zealand stream, this is only

about half the percentage given by Petersen & Cummins (1974) for animal processing of leaf packs in North America (Winterbourn, 1976).

In an analysis of trophic organisation in New Zealand stream communities (Winterbourn, 1978d) Winterbourn suggested that the lack of shredders in New Zealand could have a biogeographical basis and/or be a consequence of the nature of the terrestrial flora (e.g., its [un]palatability) which represents the assumed major source of energy to the communities.

It is at this juncture that I began the formulation of my dissertation research plans and was influenced by the unique findings of the Canterbury research group up to this point, 1978. My research plans developed in a stepwise fashion, one set of experiments leading to the next after interpretation of the first set; but overall the research programme had three basic aims. These were to address three questions: (1) Why are shredders rare in New Zealand streams and what determines their sporadic occurrence? (2) If shredder populations are not abundant in New Zealand forest streams and therefore are not operating as intermediaries in movement of carbon through food chains (as discussed above), then what are the major carbon pathways which support the large numbers of invertebrates found in New Zealand streams? (3) What is the relative significance of allochthonous and autochthonous material as a source of energy utilised by benthic invertebrates in contrasting stream types?

The role of shredders in leaf litter decomposition and the factors determining their presence and absence were examined using a comparative approach; two streams, one with and one without a resident population of shredders being used as experimental sites.

In approaching the second question, the suggestion of Winterbourn (1976) that the organic layers which form on hard surfaces (Madsen, 1972) could be the major food source for many New Zealand stream invertebrates was taken as the starting point. I investigated the structure and function of the organic layer and considered its potential as an alternative carbon pathway in stream ecosystems. Stable carbon isotope analysis was used to answer the question of differential utilisation of allochthonous and autochthonous inputs in contrasting streams. This technique allowed clear linkages between animals and their food sources to be determined.

I also investigated the relationship between stream geomorphology, forest type as well as geographic location in relation to the distribution

of aquatic invertebrate communities (using functional feeding groups [Cummins, 1974]) using a broad survey technique throughout New Zealand. The goal of this research was to examine forest stream invertebrate linkages in order to develop sound suggestions for catchment management. Results are presented as a series of four research papers and two discussions. The first discussion is in the form of a paper published in *New Zealand Journal of Marine and Freshwater Research* during the course of my thesis research with my supervisor, Dr M.J. Winterbourn, and Dr Brent Cowie, formerly a graduate student in our research group. This paper presents our combined ideas on the structure and function of New Zealand ecosystems, my own contribution being primarily in those sections dealing with elaboration of carbon pathways, geomorphology and retention and the organic layer. The second discussion (Chapter VII) provides a synthesis and general overview of my research programme and places its findings in a broader context.

Each of the four research papers is written in a form as for publication and for this reason some repetition has been inevitable.

In order to establish clear links between papers, small bridging sections have been provided where appropriate.

CHAPTER II

LEAF PROCESSING IN TWO CONTRASTING BEECH FOREST STREAMS: EFFECTS OF PHYSICAL AND BIOTIC FACTORS ON LITTER BREAKDOWN

INTRODUCTION

Many contemporary stream ecologists view stream ecosystems as processors of organic materials (Fisher, 1977, see references therein). Both allochthonous and autochthonous materials are utilised to varying degrees in streams of all sizes. However, in small forested streams it has been suggested that benthic animal communities depend on allochthonous inputs in the form of leaves, twigs, wood, etc. in varying stages of decomposition and breakdown as their primary souce of energy (e.g., Cummins, 1974). If so, studies of decomposition and sites associated with heterotrophic processes are of fundamental importance if an understanding of stream ecosystem function is to be obtained. The thrust of most research to date has been to examine the breakdown of allochthonous inputs, particularly leaf litter, and to a lesser degree wood (Anderson *et al.*, 1978) in relation to physical and biological factors (see Anderson & Sedell, 1979 for a review).

The principal physical parameters investigated have been temperature, flow rate and water chemistry. Reice (1974) found that weight losses of decomposing leaf litter increased with increasing temperatures whereas Reice (1977), Triska & Sedell (1976) and Short *et al.* (1980) found that processing rates of several leaf species were faster at lower temperatures suggesting that temperature was just one (and not necessarily the most important) parameter affecting disappearance rates. In the laboratory, weight losses caused by leaching have been shown to increase with increases in temperature from 3 to 80°C (Nykvist, 1959). However, using a lesser and more realistic environmental temperature range Petersen & Cummins (1974) found no significant difference in the amount or rate of leaching at several temperatures in the laboratory.

Reice (1974) found that water velocity did not directly affect the rate of leaf litter breakdown, but he noted that its indirect effects (e.g., creating different oxygen regimes, structuring of different biological communities) could be important in this respect. For example, he found (Reice, 1974) that weight losses increased with increasing substrate particle size (which can be affected by flow conditions) while Herbst (1981) found that buried leaf litter lost weight more slowly than surface incubated leaves.

Conflicting evidence concerning effects of dissolved nutrient concentrations on leaf decomposition rates also are available. Some workers (Hynes & Kaushik, 1969; Kaushik & Hynes, 1971; Howarth & Fisher,

1976; Elwood *et al.*, 1981) have found that leaf breakdown rates increased under conditions of N and/or P enrichment in the laboratory and the field, but Triska & Sedell (1976) found that large scale nitrate additions to a series of experimental channels did not accelerate weight losses from leaf packs.

The roles played by invertebrates in bringing about weight losses of litter have received more attention than physical factors, and numerous workers have demonstrated that large particle detritivores, shredders, can influence litter breakdown rates (Cummins *et al.*, 1973; Petersen & Cummins, 1974; Anderson & Grafius, 1975; Davis & Winterbourn, 1977). Some workers have tried to separate the biotic and abiotic components of breakdown (Petersen & Cummins, 1974) and also to separate the biological components into those performed by macro- and micro-consumers. The latter has been done either by altering shredder densities (Cummins *et al.*, 1973) or by excluding macroconsumers by enclosing leaf litter in fine meshed bags (Winterbourn, 1978c; Anderson & Sedell, 1979; McCammon, 1980).

The nutritional value of decaying litter to aquatic detritivores has also been the subject of several studies (e.g., Bärlocher & Kendrick, 1973a, b; Cummins, 1974). Cummins (1974) suggested that the micro-organisms which colonise litter serve as the major protein and carbon source for shredders with the non-living detritus acting primarily as an inert substrate. However, more recent work on aquatic insect feeding and digestion (Iverson, 1974; Baker & Bradnam, 1976; Winterbourn, 1982) has shown that some structural components of leaf detritus also are utilised as food. In general, leaf litter is viewed as a major site of energy transfer to the stream invertebrate community and concepts of stream carbon pathways have developed with leaf litter processing by large particle detritivores given a critical role in the provision of fine organic particles upon which large populations of collector organisms depend (Hynes, 1975; Short & Maslin, 1977; Grafius & Anderson, 1979).

New Zealand provides an excellent opportunity to investigate the role of shredders in leaf litter processing since shredders are absent or rare in many small forested streams, but present in large numbers in others (few streams appear to fall in between). In the present study, breakdown rates of leaf litter were compared in the two types of streams. Fine- and coarse-mesh leaf litter bags were used at both sites and comparisons were also made of breakdown rates in buried and surface

incubated bags. This work involved weight loss determinations, estim of leaf protein content, oxygen consumption of the decomposing leaves and enumeration of the invertebrate fauna associated with the decomposing litter. A further aim of this study was to try and determine the reasons why shredders were abundant at one of the chosen experimental sites but not the other.

STUDY SITES

The two study sites selected were in the Cass - Arthurs Pass region east of the main alpine divide in the Waimakariri River catchment, South Island, New Zealand. Vegetation in this region is mainly tussock-grassland but small stands of mountain beech, *Nothofagus solandri* var. *cliffortioides*, through which both study streams flow, are found in gullies and appear to be remnants of formerly extensive forests (Burrows, 1960).

Middle Bush Stream, located at 43°02'S, 171°46'E in the Cass Basin, is a first order stream which drains a 28 ha catchment of subalpine scrub, tussock and bare scree. It also includes a 3-4 ha stand of mountain beech through which Middle Bush Stream flows. The stream arises from a spring source at 850 m a.s.l. and enters the forest at 700 m a.s.l.

In the forest the stream is well shaded with a rough boulder-strewn bed and steep banks (Figure 2.1). Logs and branches on the stream bed often trap debris and inorganic sediments. Leaf and twig litter falls continuously throughout the year (Winterbourn, 1976) and often during long periods of low discharge, considerable allochthonous organic debris accumulates in pools and behind obstructions in the stream. Large organic debris is widely scattered within the stream and much of the leaf litter is swept away during major floods.

Both particulate (Winterbourn, 1976) and complete annual organic energy budgets (McCammon, 1978) have been constructed for Middle Bush Stream and several studies have been made on the ecology and life history of its invertebrate fauna (Winterbourn & Davis, 1976; Winterbourn, 1978b; Cowie & Winterbourn, 1979; Winterbourn, 1982). Autochthonous primary production is low (Cowie, 1980).

Rainfall averages about 1300 mm per year and in the long term is evenly distributed throughout the year. However, monthly variations may range from 25 - 250 mm (McCammon, 1978), and during the current study averaged 135 mm per month with a range of 50 mm to 304 mm per month.

Figure 2.1 Middle Bush Stream flowing through mountain beech forest. Note the organic debris jams and large rocks which appear as stable retention devices and flow deflectors in the channel.

Figure 2.2 Craigieburn Cutting Stream flowing through mountain beech forest. Note the steep banks, mass wasting of sediment into the channel along with large depositional areas of gravel, sand and silt on the lower banks. The stream bed is unconsolidated at this site and is easily moved during floods.

Stream discharge within the forest ranges from about 1 to 50 $\ell.sec^{-1}$ with a mean daily discharge about 5 $\ell.sec^{-1}$ (McCammon, 1978).

The second study site was on Craigieburn Cutting Stream which is located 14 km south of Middle Bush Stream at 43°09'S, 171°45'E. It is a slightly larger, second order stream draining a catchment of about 75 ha and, like Middle Bush Stream, the catchment consists mainly of subalpine scrub and scree and includes a 13 ha remnant stand of mountain beech through which the stream flows and where the study site is located. Here the stream is well shaded with little apparent autochthonous production (unpublished data). While not quantified, allochthonous forest inputs appeared to be similar if not greater in quantity to those entering Middle Bush Stream (Figure 2.2). Despite these similarities, the stream bed and banks were very different from those of Middle Bush Stream. Bed type was generally unconsolidated fine gravels which were highly mobile in many places. The upper banks were raw and exposed and subject to frequent mass-wasting of sediments into the stream channel. Debris jams and retention devices were scarce and, unlike Middle Bush Stream, most wood debris had been washed out of the lower channel onto the upper banks.

No data on rainfall or discharge are available for the Craigieburn catchment. However, rainfall could be expected to be similar to that at Middle Bush Stream while my observations indicate that discharge is similar or a little higher in flood times and as low as 1.8 $\ell.sec^{-1}$ during summer low flow conditions.

Nutrient concentrations in stream water samples from both sites were low (PO_4 0.034 - 0.047 $g.m^{-3}$; NO_3 0.02 - 0.06 $g.m^{-3}$), but the water at Craigieburn Cutting Stream was a little softer (Craigieburn Cutting Stream - 19 $g.m^{-3}$ $CaCO_3$; Middle Bush Stream - 37 $g.m^{-3}$ $CaCO_3$). Temperature regimes at the two sites were similar and were usually within 1 or 2°C. Further details of Middle Bush Stream water chemistry are given by Cowie & Winterbourn (1979).

MATERIALS AND METHODS

Leaf Bag Studies

I used leaf bags (as opposed to unenclosed packs) to estimate leaf breakdown rates because their use enables the investigator to exclude selected components of the fauna and so begin to evaluate their effects. I recognise that leaf bags can have a number of disadvantages - reduce

water exchange rates, possibly create anaerobic conditions, clog with fine particles and prevent abrasion which may be an important factor in leaf breakdown (Petersen & Cummins, 1974). For these reasons, unenclosed leaf packs have been advocated by Petersen & Cummins (1974) and Herbst (1980). Because mountain beech leaves are very small and not easily made into packs, because bags rather than packs should provide better estimates of leaf breakdown in pools (Cummins *et al.*, 1980) where shredders predominantly occur and since one of my main objectives was to examine the role of invertebrates in leaf breakdown, the bag method was chosen for this work.

Mountain beech leaves (*Nothofagus solandri* var. *cliffortioides*) collected from a recently fallen tree at Cass in December 1978 were used in leaf bag experiments. Leaves were oven-dried (60°C) for at least 72 h and weighed into 4 g lots. These were placed in heat-sealed 3 mm mesh plastic bags or 4 cm diameter tubular PVC containers closed at each end with 0.2 mm mesh. Three bags and three tubes were placed in each of 36, 5 mm mesh "Onion bags" (a total of 108 bags and 108 tubes) and tethered in Middle Bush Stream or Craigieburn Cutting Stream. For convenience, fine-mesh tubes and coarse-mesh bags will now both be referred to as fine and coarse-mesh bags. Half the bags at each site were buried at least 10 cm below the surface in depositional areas where substrates were loosely assorted cobbles (5-10 cm diameter). All other bags were placed on the bed surface in areas where they would remain submerged throughout the study. All bags were tied to bankside trees with nylon cord to prevent their being washed away.

After 24 h, one surface and one buried "Onion bag" were removed from each stream, placed in a polythene bag and taken to the laboratory in a cool polystyrene container. Thereafter, bags were collected at two week intervals for the first 12 weeks and then after 16 and 22 weeks.

Immediately upon arrival at the laboratory (*ca.* 3-4 h after collection) leaves were taken from the fine-mesh tubes and gently washed to remove attached sediments. Oxygen uptake by leaves in filtered stream water (0.45 µm) was determined with a Gilson Differential Respirometer. Measurements were made on four subsamples (each approximately 250 mg [dry weight]) from both buried and surface incubated bags from each site, and two controls (no leaves) placed at each end of the respirometer. After loading the respirometer, samples were allowed to equilibrate for 1.5 h at ambient stream temperature with the shaking motor on a low setting (3). After this, measurements were taken at three minute intervals for 1-3 h.

Leaves from the respiration flask and any leaf material remaining in the five tubes were dried at 40°C for 72 h and weighed to 0.01 g.

The contents of coarse-mesh bags were washed in sorting trays, invertebrates were removed and stored in 70% EtOH for later counting and identification and leaves were oven-dried and weighed as above.

Protein content of leaf material was determined using the extraction technique described by Kaushik & Hynes (1968) and the method of Lowry *et al.* (1951). Bovine albumin standards were used for calibration. Five subsamples of leaf material were removed from both buried and surface bags at both study sites for protein determinations.

Water temperature of each stream was recorded throughout the study period with maximum-minimum thermometers accurate to 1°C. Chemical analyses were carried out by Chemistry Division, D.S.I.R., Christchurch on water samples collected from Craigieburn Cutting Stream and Middle Bush Stream on 1 February 1979.

Food Choice Experiments

Final instar larvae of the caddisfly *Zelandopsyche ingens* (Oeconesidae) were collected from Middle Bush Stream during February and March 1979 and maintained in a small flow-through perspex aquarium at about 13°C with stream-conditioned beech leaves as food. Fifty larvae of similar size were used in all experiments. About 48 h before the start of an experiment larvae were placed individually in plastic feeding containers (11 × 15 × 7 cm) to clear their guts and to acclimatise them to the experimental conditions. Approximately every 4 h during the gut clearance period and subsequently, air was bubbled into each container to ensure an adequate oxygen supply.

Beech leaves offered to larvae had been kept in fine-mesh (0.2 mm) covered tubes in Middle Bush Stream for varying periods so that on 18 May 1979 when the experiments were begun, leaves which had been stream-conditioned for two days, and two, six and ten weeks were available.

Leaves of each type (degree of conditioning) were tied together with nylon thread in groups of six, tagged for later identification, and wet weighed to 0.1 mg. Groups of leaves were offered to larvae in all possible combinations, each combination being replicated five times. In addition, ten groups of each leaf type were placed in feeding containers without larvae to determine weight losses over the experimental period which were not due to insect feeding.

At the end of trials, which lasted 60 h, the leaves remaining on the tether and in the leaching controls were removed, dried as above and weighed to the nearest 0.1 mg. Wet:dry weight ratios were determined on ten subsamples of each leaf type to enable total dry weight of leaf ingested to be calculated from initial leaf wet weights.

Zelandopsyche ingens Transplant Experiment

On 5 January 1979, 75 F-1 and F-2 *Z. ingens* larvae were collected from Middle Bush Stream. They were divided into three equal groups consisting of 15 F-1 and 10 F-2 larvae. One group was placed immediately in 10% formalin whereas the other two groups were placed in wire framed cages (surface area 0.2 m^2) covered with 1 mm mesh nylon netting.

Cages were placed in Middle Bush Stream and Craigieburn Cutting Stream with leaf litter collected from the respective streams added as food.

On 23 March 1979, i.e., after 77 days, larvae were taken from the cages, preserved in formalin and identified to instar. Along with the initially preserved larvae (5 January) they were oven-dried for 72 h at 60°C and weighed to the nearest 0.1 mg.

Coarse Benthic Detritus and Invertebrate Surveys

Stored benthic coarse particulate organic matter (CPOM) (>1 mm) and benthic invertebrates were sampled twice at Middle Bush Stream and Craigieburn Cutting Stream in 1981. The first survey was carried out in early autumn (9 April 1981) after a long dry period and the second in mid-winter (24 July 1981) following a period of high discharge. CPOM and invertebrates were collected using a 0.1 m^2 Surber sampler with a 0.5 mm mesh net. Larger debris in the sampling area was removed by hand and later oven-dried and weighed. Each survey consisted of 15 samples taken at 5 m intervals within the section of stream where leaf bag studies were conducted. Notes on site characteristics including substrate type, depth, flow conditions and degree of siltation were taken.

Stream Bed Mapping and Wood Debris Surveys

At each study site approximately 100 m of stream channel including upper banks and associated large organic debris were mapped just before the first CPOM survey. Characteristics of stream bed including pool

depth, types of stored materials and sediment size were noted on maps as well as other features of the lower and upper banks. The volume of wood debris in the channel was determined using Van Wagner's (1968) line intersect method used in forest fuel sampling.

RESULTS

Stream Geomorphology and Distribution of Wood

Detailed stream bed maps (Figures 2.3 and 2.4) and photographs of the two sites (Figures 2.1 and 2.2) clearly demonstrate the contrasting nature of the two stream beds. Craigieburn Cutting Stream had a very unstable bed with large quantities of gravel, sand and silt continually moving into and down the stream channel. The bed consisted of long, shallow, unstable riffles which retained little leaf litter. Few large stones, boulders, or wood debris jams which could act as retention devices were present and most of the wood present occurred not in the stream channel but on the upper banks. Debris jams in March 1981 numbered six per 100 m at the study site while wood volume in the channel was 100 $cm^{-3}.m^{-2}$. Stream bed material was loose with poor particle packing and few stable interstitial spaces.

In contrast, Middle Bush Stream is comparatively stable with less mass-wasting into the channel and associated bank undercutting and more stone and wood retention devices. The stream channel contained 16 debris jams per 100 m in March 1981. This compares with Bilby & Likens (1980) estimate of approximately 14 debris jams per 100 m for a first order, forested New England stream. Volume of wood on the stream bed was 900 $cm^{-3}.m^{-2}$. The bed material was generally well packed and had many more interstitial spaces than Craigieburn Cutting Stream.

Benthic CPOM Abundance

Estimates of the amount of CPOM on the beds of the two streams on two occasions in 1981 are shown in Table 2.1. The survey made in April 1981 was carried out following a long period of low summer flow and represents several months of litter accumulations without major flushing events. In contrast, the July survey was made shortly after a period of high water which had flushed out the two study sites.

Figure 2.3 Scale map of a 40 m reach of Middle Bush Stream study site showing wood debris in and overhanging the channel as well as other prominent physical features of the site.

Middle Bush Stream

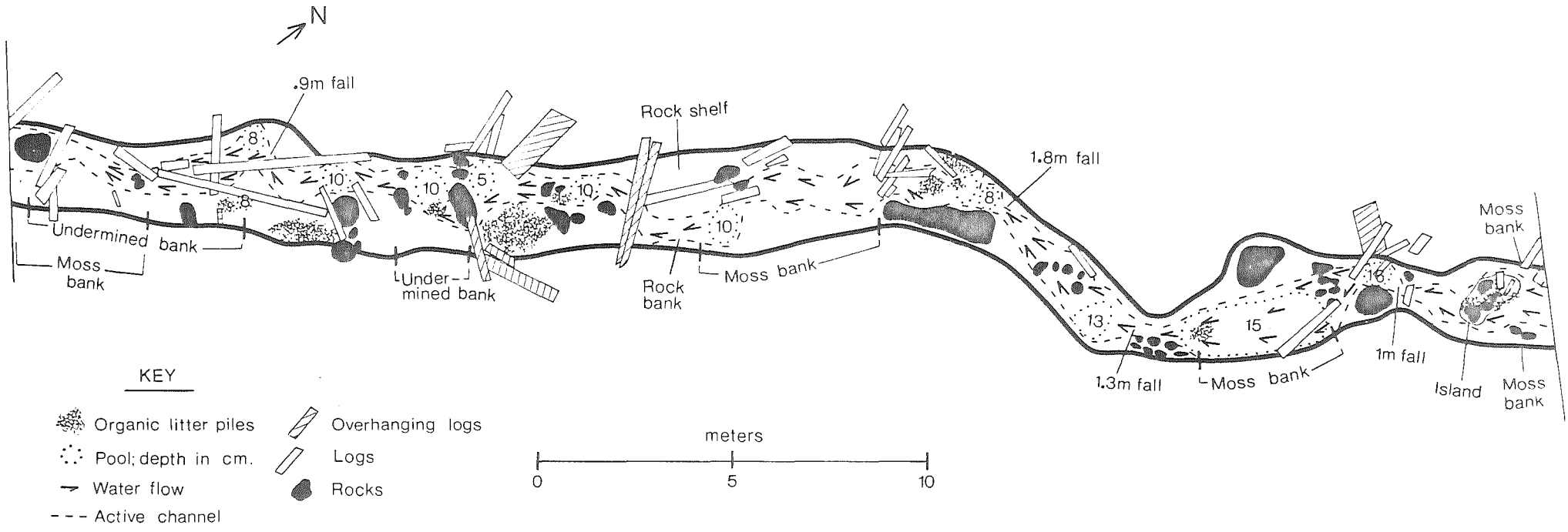


Figure 2.4 Scale map of a 40 m reach of Craigieburn Cutting Stream study site. Key and scale as in Figure 3.

Craigieburn Cutting Stream

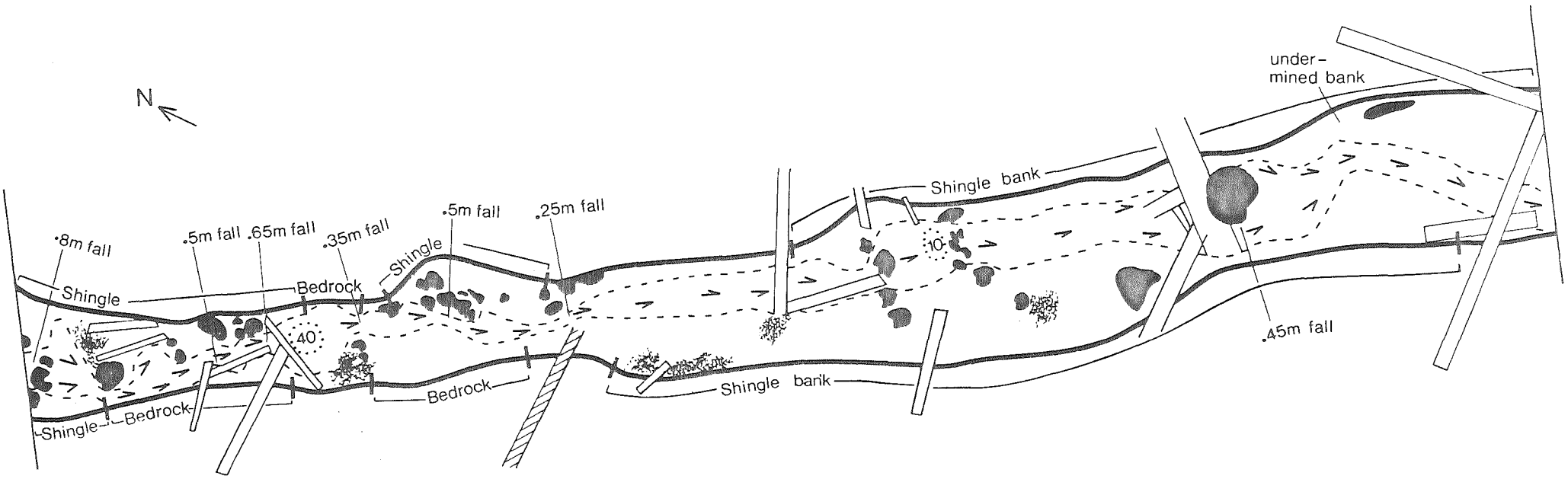


Table 2.1 Mean amounts ($g.m^{-2}$) of stored benthic CPOM in early autumn and mid-winter samples. Significance level between the two streams determined by Mann-Whitney U test.

	Middle Bush Stream	Craigieburn Cutting Stream
Early Autumn Sample		
Mean wt of CPOM ($g.m^{-2}$)	495.7	107.6
(ranges)	(17.0 - 3843.3)	(8.1 - 850.4)
	n = 15	n = 15
Significance level	$P < 0.01$	
Mid-Winter Sample		
Mean wt of CPOM ($g.m^{-2}$)	107.6	26.9
(ranges)	(0.8 - 510.3)	(0.2 - 177.2)
	n = 15	n = 15
Significance level	$P < 0.01$	

Dry weight of CPOM was significantly higher ($P < 0.01$, Mann-Whitney U test) in Middle Bush Stream than in Craigieburn Cutting Stream both before the winter freshets and after. However, benthic CPOM levels decreased markedly at both sites as a result of flooding. It is interesting to note that winter benthic CPOM levels were *ca.* 22% of late summer levels at both sites even though Middle Bush Stream had higher initial benthic CPOM levels. Since both streams receive similar amounts of litter annually (at least via leaf-fall vectors) the difference in late summer levels can best be accounted for in terms of bed retentiveness which is much more effective at low discharges in Middle Bush Stream.

Faunal Characteristics of the Two Sites

The invertebrate fauna of Middle Bush Stream was dominated by larval insects. Thirty-three taxa excluding Chironomidae were distinguished in the faunal samples with Trichoptera and Plecoptera best represented (Table 2.2). Several large and small particle detritivores were abundant at Middle Bush Stream including the caddisfly *Z. ingens* and the plecopterans *Austroperla cyrene*, *Spaniocerca zelandica* and the mayfly *Deleatidium* sp.

Table 2.2 Macroinvertebrates taken in benthic samples in Middle Bush Stream and Craigieburn Cutting Stream, April and July 1981. Percentage composition values are calculated for the two months combined. * denotes less than 1% of the total fauna. Invertebrates which did not exceed a mean of ≥1% at either site are not shown. Invertebrate feeding mode is represented as follows: CB - collector-browser; P - predator; S - shredder.

Invertebrates	Middle Bush Stream (% of fauna)	Craigieburn Cutting Stream (% of fauna)	Feeding Mode
Oligochaeta			
Eiseniella tetraedra	2.2	*	CB
Insecta			
Ephemeroptera			
Deleatidium sp.	42.9	59.7	CB
Nesameletus sp.	5.1	22.0	CB
Plecoptera			
Austroperla cyrene	1.5	*	S
Cristaperla fimbria	1.8	*	CB
Spaniocerca zelandica	10.0	4.3	CB
Zelandobius sp.	5.6	*	CB
Trichoptera			
Hydrobiosella sp.	3.5	*	CB
Olinga feredayi	2.6	1.9	CB
Philorheithrus agilis	3.0	*	P
Rhyacophilidae	3.2	1.6	P
Zelandopsyche ingens	4.7	Absent	S
Mecoptera			
Microchorista philpotti	1.1	*	P
Diptera			
Tipulidae	3.2	2.4	CB
Coleoptera			
Elmidae	*	2.4	CB
Helodid Species A	1.5	*	CB
Hydraenidae	1.8	1.7	S

Twenty-eight taxa, all of which were present in Middle Bush Stream were recorded from Craigieburn Cutting Stream. However, densities and species richness of most samples were lower. A notable difference at Craigieburn Cutting Stream is the absence of the large shredding caddisfly and stonefly, *Z. ingens* and *A. cyrene*, which are so abundant at Middle Bush Stream. The absence of these and other large particle detritivores

at Craigieburn Cutting Stream makes this site typical of many other forested New Zealand streams (Winterbourn *et al.*, 1981).

Zelandopsyche ingens Transplant

This experiment was designed to see whether larvae of *Z. ingens*, which are not found in Craigieburn Cutting Stream, could survive and develop normally there. Each of the initial three groups of larvae used consisted of 10 F-2 and 15 F-1 larvae (Table 2.3). Larvae in the initial group, which were preserved at the start of the experiment, had a mean dry weight of 2.6 mg ± 1 SD 1.7 mg. After 77 days (which coincided with the rapid growth phase of *Z. ingens* in Middle Bush Stream [Winterbourn & Davis, 1976]), 23 final and 2 F-1 (mean weight 19.3 mg ± 1 SD 8.9 mg) were recovered from the Middle Bush Stream cage and 23 final instar larvae and two empty final instar cases were found in the Craigieburn Cutting Stream cage (mean weight = 25.1 mg ± 1 SD 9.8 mg).

Table 2.3 Instars and mean weights of the three groups of *Zelandopsyche ingens* larvae at the beginning and end of the transplant experiment.

	Initial Sample	Middle Bush Stream	Craigieburn Cutting Stream
Date	5 Jan. 1979	23 March 1979	23 March 1979
Instars	F-2 × 15	F × 23	F × 23
	F-1 × 10	2 empty final instar cases	F-1 × 2
Mean wt (mg) ± 1 SD	2.6 ± 1.7 n = 25	19.3 ± 8.9 n = 23	25.1 ± 9.8 n = 25

Growth rates at both sites were similar to those calculated for field populations of *Z. ingens* in Middle Bush Stream (Winterbourn & Davis, 1976; Winterbourn, 1982). It is clear that larvae can grow equally well in both streams and their absence from Craigieburn Cutting therefore does not appear to be associated with peculiarities of water chemistry or food quality *per se*. Rather it appears to be related to the organic matter retention capacity of the streams; a point to be discussed later.

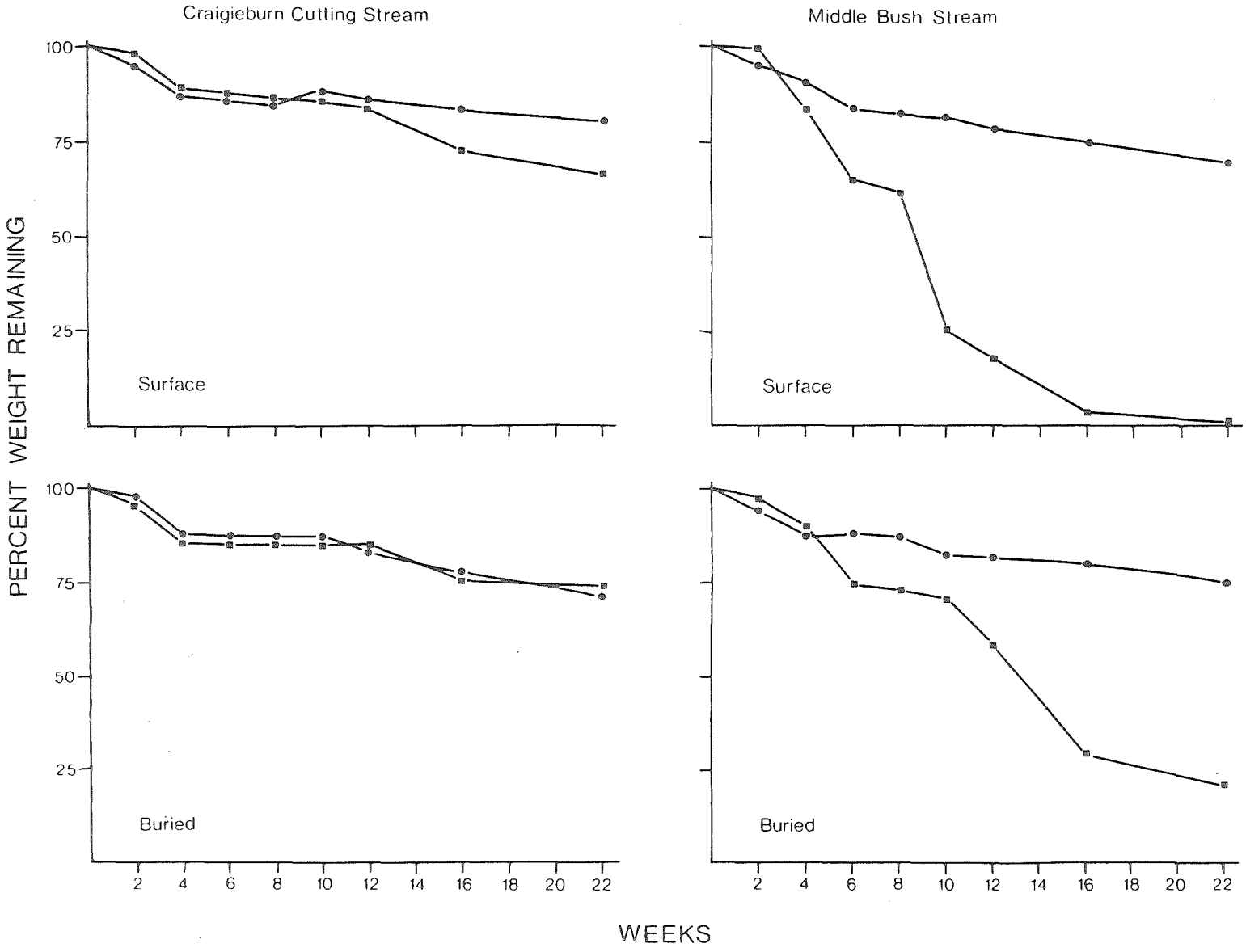
Leaf Litter Breakdown

Leaf weight losses averaging 1.2 and 1.0% of initial dry weight occurred as a result of initial 24 h leaching in Craigieburn Cutting Stream and Middle Bush Stream respectively. Subsequent losses of weight varied considerably between sites, buried and surface bags, and between containers of different mesh size (Figure 2.5). In Middle Bush Stream, coarse-mesh surface bags lost weight far more rapidly than their fine-mesh counterparts, particularly after eight weeks of immersion. After 22 weeks, coarse-mesh, surface incubated bags were empty of leaf material while the fine-mesh bags still had approximately 69% of their leaf material (by weight) remaining. Leaves in buried bags at Middle Bush Stream exhibited similar weight loss patterns to those in surface bags but with a slight time lag. Leaves in buried, coarse-mesh bags lost weight more rapidly than those in buried fine-mesh bags, a trend that was most pronounced after ten weeks of immersion. Also, leaves in coarse-mesh bags had not disappeared completely after 22 weeks, when approximately 22% of the material remained.

Differences in weight loss patterns between coarse- and fine-mesh bags at Craigieburn Cutting Stream were slight (Figure 2.5). Leaves in surface incubated coarse- and fine-mesh bags lost weight at approximately the same rate for the first 12 weeks after which the loss rate from coarse-mesh bags increased. However, the amount remaining in surface incubated bags at the end of the experiment was substantially higher than in surface bags at Middle Bush Stream (Craigieburn Cutting Stream, fine mesh = 81%, coarse mesh = 66%). Leaves in buried coarse- and fine-mesh bags at Craigieburn Cutting Stream exhibited minimal differences in weight loss patterns between themselves compared to Craigieburn Cutting Stream surface bags. Weight loss differences between buried coarse, and buried fine-mesh bags were even less than between surface incubated fine- and coarse-mesh bags.

Leaves in both surface and buried coarse-mesh bags in Middle Bush Stream lost substantially more weight than their Craigieburn Cutting Stream counterparts. However, weight losses from fine-mesh bags were similar in both streams, although slightly lower in those that were buried. It is particularly interesting to note that at Craigieburn Cutting Stream, leaves in coarse-mesh bags which permitted macroconsumers access, had similar weight loss patterns to leaves in fine-mesh bags at Middle Bush Stream from which macroinvertebrates were excluded. This suggests that macroconsumers

Figure 2.5 Percentage leaf weight remaining in mesh bags incubated on the stream bed and buried 10 cm in the substrate at Craigieburn Cutting Stream (left) and Middle Bush Stream (right). 1.S.E. of the mean never exceeded 7% of the range (n = 3) at any sampling date. ● - fine-mesh bags (0.2 mm) ■ - coarse-mesh bags (3 mm)


Craigieburn Cutting Stream
Middle Bush Stream
PERCENT WEIGHT REMAINING
100
75
50
25
Surface
Buried
2
4
6
8
10
12
14
16
18
20
22
WEEKS

significantly influence weight losses in coarse-mesh bags at Middle Bush Stream but not in Craigieburn Cutting Stream. Direct observations of leaves agree with this suggestion as those from coarse-mesh bags in Middle Bush Stream showed evidence of insect chewing and fragmentation at their margins whereas leaves in fine-mesh bags at Middle Bush Stream and from all Craigieburn Cutting Stream bags showed no evidence of animal feeding and only slow epidermal tissue breakdown.

The percent protein content of decomposing leaves in surface incubated and buried bags in both streams increased between weeks two to six and remained relatively constant thereafter (Figure 2.6). Maximum percentage protein (just above 6% dry weight) was attained in surface bags in both streams while levels between 4 and 6% were found in buried bags. No increases (and in some cases slight decreases) in protein were found in the first two weeks in all treatments. This was probably the result of losses caused by initial leaching similar to the nitrogen losses reported by Triska & Sedell (1976) for four leaf species in Washington, U.S.A.

From six weeks onwards protein content of buried Middle Bush Stream bags was significantly lower ($P < 0.01$, Mann-Whitney U test) than surface incubated leaves at Middle Bush Stream; while in Craigieburn Cutting Stream surface and buried leaves were more similar in protein content.

Similar temporal patterns of oxygen consumption were obtained for buried and surface incubated leaves from both streams (Figure 2.6). Peak consumption (up to 210 $\mu\ell\ O_2 \cdot g^{-1}\ dw.hr^{-1}$) occurred at 6-8 weeks then declined to a relatively constant level after 12 weeks. The rise in oxygen consumption rate recorded after 22 weeks in Craigieburn Cutting Stream surface incubated leaves is not easy to explain and since replicate values were highly variable (Figure 2.6) it is possible that they are due (in part) to faulty Gilson technique.

In both streams, leaves taken from surface bags had higher respiration rates than leaves from buried bags indicating the presence of more active microbial populations.

Invertebrates Associated with Leaf Bags

Mean numbers of invertebrates (excluding Chironomidae) present on each sampling date in buried and surface incubated coarse-mesh bags taken from the two streams are shown in Figure 2.7. These were made up of at least 20 species (Appendix I) and included most of the common species

Figure 2.6 Oxygen consumption and protein content of mountain beech leaves incubated in Craigieburn Cutting Stream (a, b) and Middle Bush Stream (c, d). ■ - surface bags. ○- buried bags. Vertical bars represent 1.S.E. when >5% of the mean.

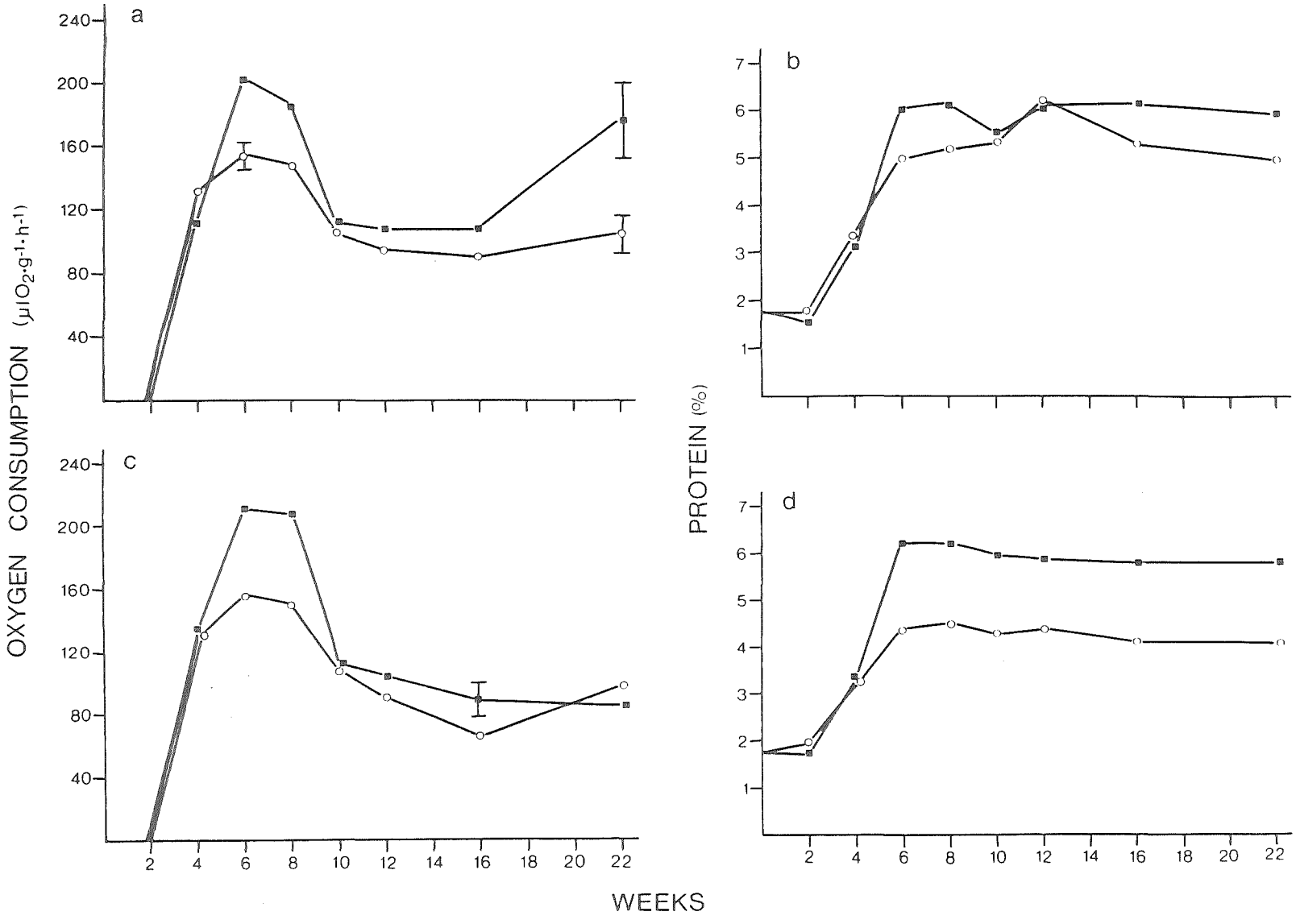
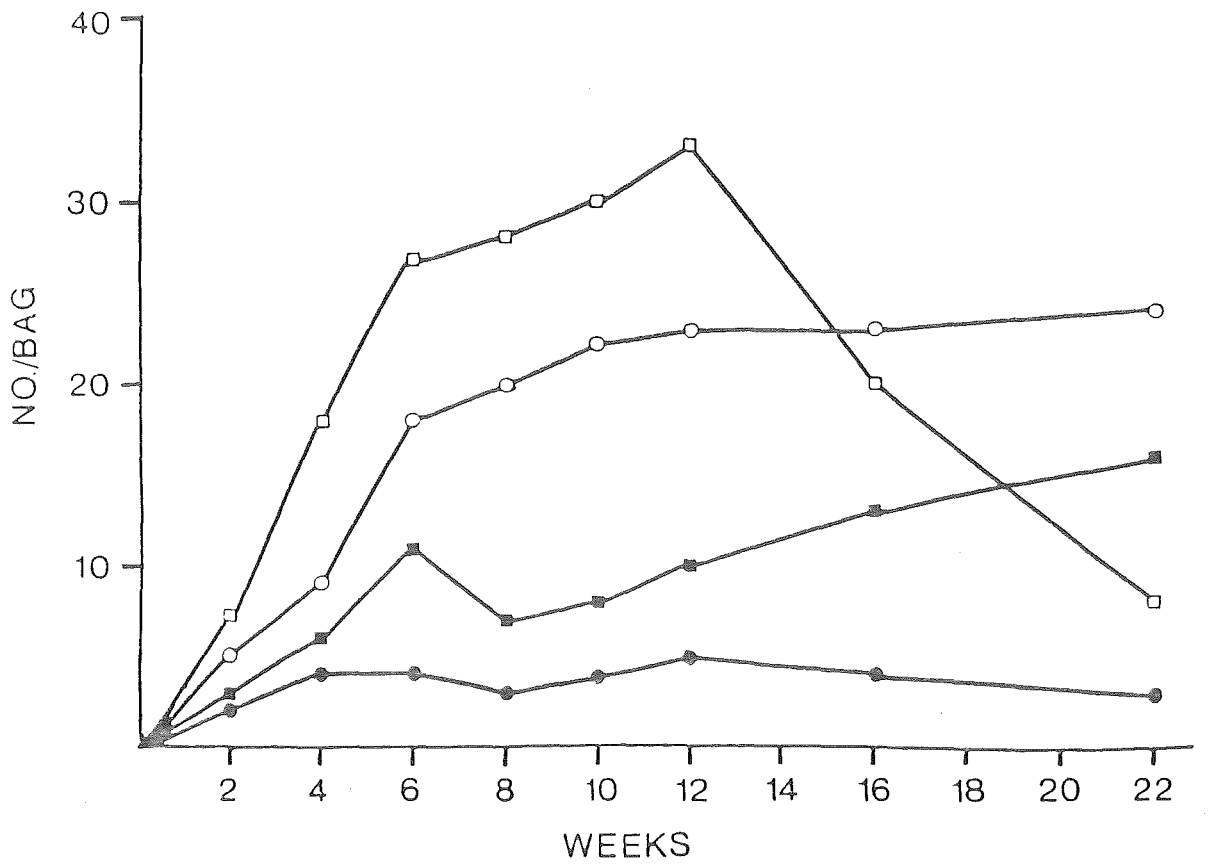

a
b
c
d
OXYGEN CONSUMPTION (µlO2·g-1·h-1)
PROTEIN (%)
WEEKS
240
200
160
120
80
40
7
6
5
4
3
2
1
2
4
6
8
10
12
14
16
18
20
22

Figure 2.7 Mean numbers of invertebrates (excluding Chironomidae) colonising 3 mm mesh litter bags (n = 3) on eight sampling occasions. Detailed information on numbers of taxa represented at each sample are presented in Appendix I. Middle Bush Stream: surface bags - □ , buried bags - ■ . Craigieburn Cutting Stream: surface bags - ○ , buried bags - ● .


40
30
20
10
NO./BAG
2
4
6
8
10
12
14
16
18
20
22
WEEKS

taken in faunal surveys. In general, surface bags at both sites were colonised by more species and more individuals than buried bags. Mean numbers of invertebrates per bag increased with time over the first 10 weeks after which they remained nearly constant in Craigieburn Cutting Stream. In Middle Bush Stream numbers of colonising insects declined towards the end of the experiment when all original leaf litter had disappeared. At this time invertebrates remaining were associated with fine particulate material and bag surfaces which provide habitat for browsing species (Winterbourn, 1978c). Invertebrate numbers in buried bags at both sites were lower than their surface counterparts with those in Craigieburn Cutting Stream containing fewer insects than those in Middle Bush Stream.

Surface incubated bags taken from Middle Bush Stream were colonised by the largest number of species. Larvae of the shredding caddisfly, *Z. ingens*, steadily increased in number to 38 per three leaf bags in week 12 but declined thereafter when little leaf material remained in the bags. Other less abundant insects which colonised the bags and are known to be at least facultative leaf shredders were the plecopterans *Austroperla cyrene*, species of Hydraenidae and Helodidae and the trichopteran *Olinga feredayi*. The most abundant fine particle browsers and scrapers present were *Deleatidium* and *Spaniocerca zelandica*. The latter were most abundant in 4-12 week incubated bags whereas the former were common at all times. All other species were represented by only a few individuals which occurred sporadically.

The shredders, *Z. ingens* and *Austroperla cyrene* also colonised buried bags taken from Middle Bush Stream but were more sporadic in occurrence and present in smaller numbers. This suggests they may have had less impact on leaf breakdown which was slower in buried bags (Figure 2.5). Fine particle detritivores were also less abundant in buried bags. In fact, the only relatively common species present in comparable numbers in surface and buried bags was the trichopteran *Philorheithrus agilis* which is primarily a carnivore.

Fewer invertebrates (species and numbers) colonised leaf bags in Craigieburn Cutting Stream than Middle Bush Stream. Most abundant species were the browsing mayflies *Deleatidium*, *Nesameletus* and the caddis *P. agilis* and apart from a single larva of the stonefly *A. cyrene* no shredders were found. The fine particle detritivore, *S. zelandica* also occurred in very small numbers in both surface and buried bags.

The absence of shredders can be correlated with the slower loss of weight by leaves held in Craigieburn Cutting Stream bags and strongly suggests that in Middle Bush Stream large particle detritivores play a major role in leaf breakdown. Further evidence supporting this contention is provided by a comparison of leaf breakdown rates between Craigieburn Cutting Stream coarse-mesh surface bags and Middle Bush Stream fine-mesh surface bags - rates which were not significantly different (Kruskal-Wallis analysis of variance).

Food Preference of *Z. ingens*

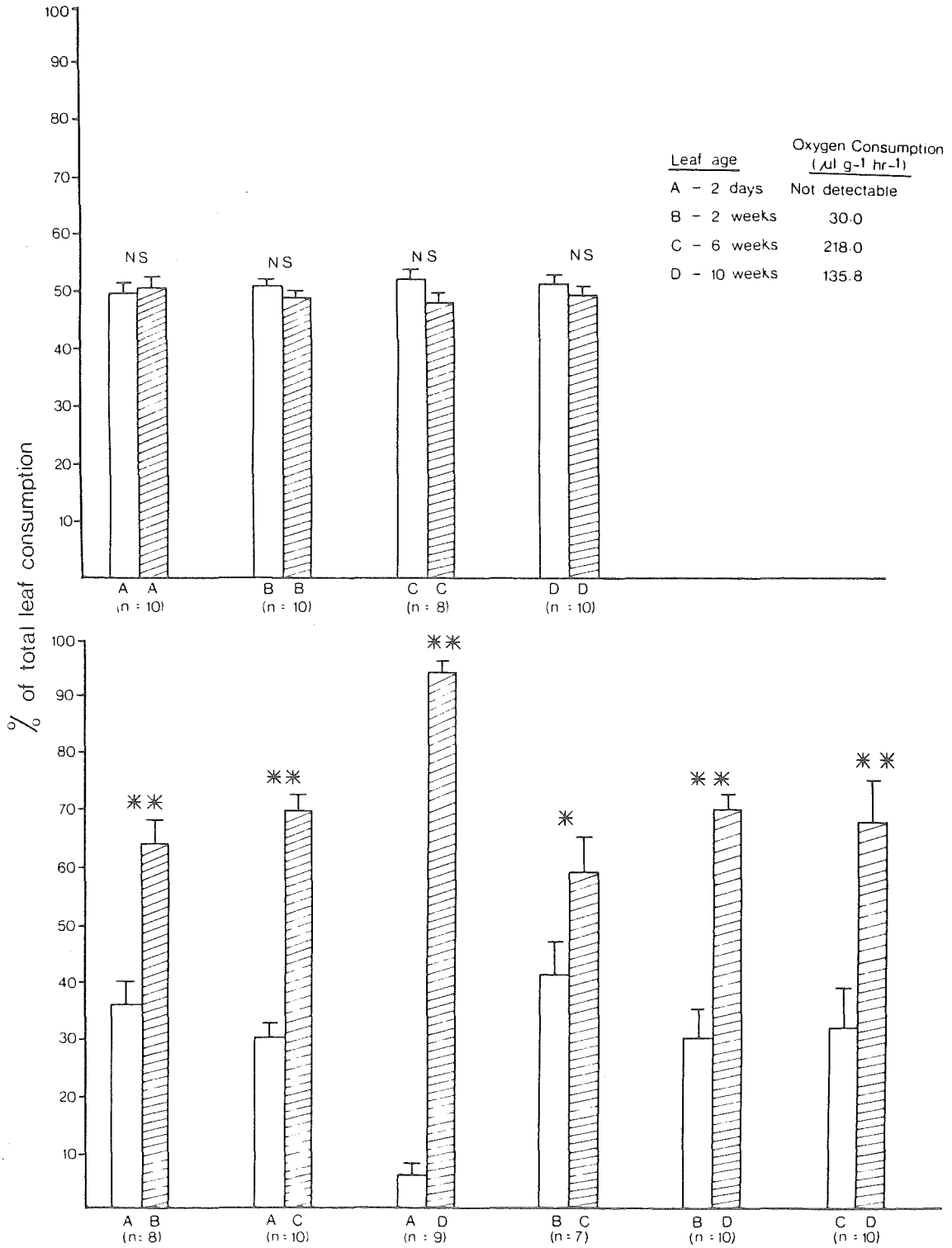
The percentage of leaf type eaten by larvae in food choice experiments and the statistical significance of results is shown in Figure 2.8. When larvae were presented with a choice of leaves of the same "age" they showed no discrimination. However, significant differences were found in the percentage of different aged leaves eaten in all other trials indicating that *Z. ingens* is a selective feeder. In all trials, larvae ate significantly more of the longer conditioned, alternative offered. Discrimination was greatest between 2 day and 10 week incubated leaves while the least was between two and six week old leaves. Larvae did not necessarily choose leaves which had the higher oxygen consumption rates (and presumably a more active microflora) (Figure 2.8) which suggests that selection could be related to leaf softness which increases with age.

DISCUSSION

My investigations in two small mountain streams of comparable size, water temperature and water chemistry, indicate that observed differences in leaf breakdown rates were associated with differences in the benthic invertebrate fauna which themselves appeared to be primarily a function of physical stream bed characteristics. Thus, weight losses from coarse-mesh (3 mm) leaf bags incubated on the bed surface in Middle Bush Stream, a relatively stable, retentive stream with a large population of shredders, were more rapid than in Craigieburn Cutting Stream where shredders were absent. On the other hand, litter breakdown rates in fine-mesh bags which excluded detritivorous invertebrates were similar in both streams and comparable to rates obtained in coarse bags at Craigieburn Cutting Stream.

Rates of weight loss in coarse-mesh bags in Middle Bush Stream were greater than those obtained in a previous study in that stream using 1 mm

Figure 2.8 Percentage of total material eaten in trials with pairs of mountain beech leaves conditioned for the same (upper) or different (lower) time periods. Conditioning times and respective oxygen consumption rates are shown in the key. Error bars are + 1.S.E. Statistical comparisons within pairs (Mann-Whitney U test): NS - not significant, * $P < 0.05$, ** $P < 0.01$.


% of total leaf consumption
Leaf age
Oxygen Consumption (µl g-1 hr-1)
A - 2 days
Not detectable
B - 2 weeks
30.0
C - 6 weeks
218.0
D - 10 weeks
135.8
NS
A A (n = 10)
B B (n = 10)
C C (n = 8)
D D (n = 10)
A B (n: 8)
A C (n = 10)
A D (n = 9)
B C (n = 7)
B D (n = 10)
C D (n = 10)

mesh bags which excluded the larger leaf-feeding insects (65 and 140 days for 50% weight loss respectively; Davis & Winterbourn, 1977), supporting the contention that the feeding activities of large aquatic insects have a major impact on leaf breakdown. In Middle Bush Stream, much of this weight loss could be attributed to a single species (*Zelandopsyche ingens*) in contrast to most other leaf breakdown studies which have indicated that several species were probably responsible for litter disappearance (e.g., Meyer, 1980; Short *et al.*, 1980).

It should be noted however, that no direct studies involving estimates of the contribution of individual shredder species to litter disappearance have been made and it is possible that even where a number of species are present, one or two (large) species could be responsible for most of the breakdown. Thus, Sedell *et al.* (1975) found that the appearance of final instar larvae of *Lepidostoma unicolor* in an Oregon stream, increased the breakdown rate of conifer needles threefold.

While leaf breakdown on the stream bed surface has been investigated by several workers, only Herbst (1980) has compared surface and sub-surface processing rates. As stream beds scour and fill, leaf material is alternately buried and exposed which makes it important that decomposition processes below the surface be examined. Additionally, Coleman & Hynes (1970) and Williams & Hynes (1974) have described an active hyporheic invertebrate community which could well affect litter breakdown below the surface.

In both Craigieburn Cutting Stream and Middle Bush Stream, breakdown of buried leaves was slower than surface breakdown, corroborating the findings of Herbst (1980). Herbst suggested several possible explanations for the observed decreases in sub-surface breakdown rates including greater compaction of buried litter resulting in a decreased surface area available for microbial colonisation, decreased abrasion resulting in reduced mechanical breakage, and the presence of anaerobic conditions which may slow decomposition rates. In my study, buried leaf bags did not appear to be under anaerobic conditions, but it is likely that reduced water exchange across the microbially colonised leaf surfaces may have caused a decrease in oxygen consumption rates, resulting in slower decomposition.

The fauna associated with buried bags was similar to that found in surface incubated bags with minor exceptions and no specific hyporheic elements were found. Litter breakdown below the surface was influenced by shredders in Middle Bush Stream and it is clear that such activity should be considered in the construction of organic matter processing budgets.

Why were shredder populations essentially absent from Craigieburn Cutting Stream in contrast to Middle Bush Stream, despite both streams having similar water chemistry, temperature regimes, flow characteristics and allochthonous inputs? I believe the key reason is the poor retention characteristics of Craigieburn Cutting Stream, retention of organic matter being essential if obligate shredders with life histories of a year or more (Winterbourn, 1978b) are to maintain viable populations. My finding that caged larvae of the shredder *Z. ingens* survived and grew equally well in Craigieburn Cutting and Middle Bush Streams, strongly supports this contention. Further, food choice experiments with *Z. ingens* demonstrated that larvae preferentially selected well-conditioned leaves, not necessarily because they provided the most nutritious food (selected leaves were not necessarily those with the highest oxygen consumption rates and therefore need not have had the largest or most active microbial populations [Ward & Cummins, 1979]) but perhaps because they become increasingly softer, the longer they were submerged.

Several physical factors contributed to the non-retentive nature of Craigieburn Cutting Stream. First, wood debris which frequently forms the basis of organic dams (Swanson *et al.*, 1976; Bilby, 1981) was scarce in the stream channel which consequently lacked many significant obstructions. Bilby & Likens (1980) found that export of coarse particulate matter from a New England stream increased 500% after (intentional) debris jam removal, and Middle Bush Stream and Craigieburn Cutting Stream can be roughly equated with their stream before and after treatment.

Second, numerous sources of gravel, sand and silt fed Craigieburn Cutting Stream and this material moved through the stream channel filling interstitial spaces and creating unstable, shifting, depositional areas which resulted in channel migration within the lower banks after high flows. Mass-wasting of the steep upper banks as well as input from the bare scree slopes above the tree line provided the main sediment sources in both streams but were far less marked in Middle Bush Stream. Also, the larger, more stable bed materials and more abundant wood debris in Middle Bush Stream acted as sediment retainers which prevented much loose material from moving far downstream until very high flows caused debris jam failure. This is in accordance with the findings of Bilby (1981) who reported a marked decrease in storage of organic and inorganic sediments after debris jam removal.

The physical conditions provided by Craigieburn Cutting and Middle Bush Streams in many ways are analogous to those provided by two Oregon streams studied by Sedell *et al.* (1975), one (WS10) with a loose rock and gravel bed and very variable flow regime, and the other (Mack Creek) with a more stable bed incorporating large boulders and debris jams. In both the New Zealand and Oregon situations, the more retentive stream supported a much larger shredder population and it can be inferred that retentiveness was primarily a function of stream geomorphology. To summarise, shredders represent an important component of the benthic fauna in Middle Bush Stream and contribute about 40% of the benthic secondary production (unpublished data).

In this respect, Middle Bush Stream conforms with the pattern described by Cummins (1974), Vannote *et al.* (1980) and others who have emphasised the role of coarse detrital inputs as primary energy sources to small forested streams.

On the other hand, <5% of the secondary production of Craigieburn Cutting Stream is provided by shredders, yet a diverse fauna of browsing invertebrates is present. Some workers have stressed the significance of shredder-produced fine particulate organic matter (FPOM) as a food source for collectors (Cummins, 1974; Short & Maslin, 1977; Anderson & Cummins, 1979). However, it is clear that various sources of FPOM other than shredder feeding must occur and that fine particles are incorporated into the organic layers which are an ubiquitous feature of submerged stone surfaces in streams. Research reported later in this thesis (Chapter III) indicates that the organic layer on stone surfaces is a primary food source for many New Zealand stream invertebrates and that dissolved organic carbon (DOC) which is readily leached from leaves is a carbon source for microbes associated with stone surfaces. This being so, streams which are non-retentive with respect to CPOM may well be very retentive (as can be inferred from leaf leachate uptake work, e.g., Lock & Hynes, 1976; McDowell & Fisher, 1976; Dahm, 1981) with respect to DOM and thereby support extensive insect populations.

In the previous chapter I showed that shredders are not necessary intermediaries of carbon flow in forest stream food webs. I suggest that streams which are not retentive with respect to CPOM may well be so with respect to DOM which is incorporated into the organic layers which occur on stone surfaces. Following the initial work of Madsen (1972) and the suggestions of Lock & Hynes (1976) and Winterbourn (1976) I will now consider the role of the organic layer as a potential site of DOM uptake and subsequent transfer to the benthos.

CHAPTER III

THE FORMATION, STRUCTURE AND UTILISATION OF STONE SURFACE ORGANIC LAYERS IN STREAMS

INTRODUCTION

Research into the feeding relationships of lotic invertebrates has intensified in recent years, concurrently with studies of stream ecosystem structure and function. Much of this work has involved the identification and quantification of carbon pathways and the measurement of energy processing rates (Cummings, 1974; Anderson & Sedell, 1979; Vannote *et al.*, 1980).

Aquatic invertebrates represent an important group of processors and considerable emphasis has been placed on the role of those classified as shredders or large particle detritivores (Cummins, 1973) since they bring about particle size reduction by their feeding activities. Numerous studies have considered the detrital-microbial complex in relation to shredder feeding (see Anderson & Sedell, 1979; Cummins & Klug, 1979 for reviews).

Many forested New Zealand stream ecosystems appear to differ markedly from their North American counterparts with respect to both structure and function (Winterbourn *et al.*, 1981). Thus, shredders are rarely abundant and therefore detrital breakdown initiated by animal feeding must be of limited importance. However, as carbon inputs are substantial in forested streams and benthic invertebrates are abundant, alternative pathways of carbon flow must assume greater significance.

Madsen (1972, 1974) suggested that the organic based film adhering to stones in streams (the organic layer) is an important food source for stonefly larvae in Denmark and Winterbourn (1976) proposed that such layers may be the major food sources of benthic invertebrates in New Zealand forest streams. Similarly, Calow (1975) and Pennak (1977) have noted the potential food value of organic layers and a positive correlation between small invertebrate biomass and organic layer ATP was reported by Barton & Lock (1979) from a deep river in northern Canada.

In this paper, the composition, formation, metabolism and utilisation of stone surface organic layers produced under field conditions and in the laboratory is reported. Particular attention is paid to "heterotrophic" layers grown in the dark and from which algae were excluded.

MATERIALS AND METHODS

Field Sites

Field studies were made at two sites at Cass in the South Island of New Zealand. One was on Middle Bush Stream which runs through a stand of mountain beech (*Nothofagus solandri* var. *cliffortiodes*) and the other was at the mouth of a small constant temperature (10°C) spring which flowed into Grasmere Stream. The environment of Middle Bush Stream has been described in detail in Chapter II and by Winterbourn (1976). The stream is well shaded, receives substantial inputs of allochthonous detritus and supports low levels of autochthonous primary production. Water column dissolved organic carbon (DOC) levels average 5 $g.m^{-3}$ ($mg.\ell^{-1}$).

The spring site was located at the base of a scree and tussock covered hillside. It received direct sunlight, allochthonous inputs appeared to be negligible and DOC concentration of spring water was <0.5 $g.m^{-3}$.

At each site, experimental channels were used for organic layer studies. The Middle Bush channel was sited alongside the stream and was gravity fed by water drawn from a weir (Figure 3.1). The channel was not subjected to flooding like the parent stream and so enabled undisturbed experimental work to continue at all times. The spring site channel was placed up against the spring vent so that water flowed directly into it (Figure 3.2). Water depth in both channels was about 3 cm and current speed about 4 $cm.s^{-1}$. At both sites one longitudinal half of each channel was covered with wood or black polythene so that dark-light comparisons could be made.

Layer Formation in the Dark

Graywacke stones cut to three different shapes and sizes with a diamond saw (cubes 2.25 cm^2 face; flat slabs 16 cm^2 and rock chips glued to aluminium scanning electron microscope stubs) acted as surfaces for colonisation.

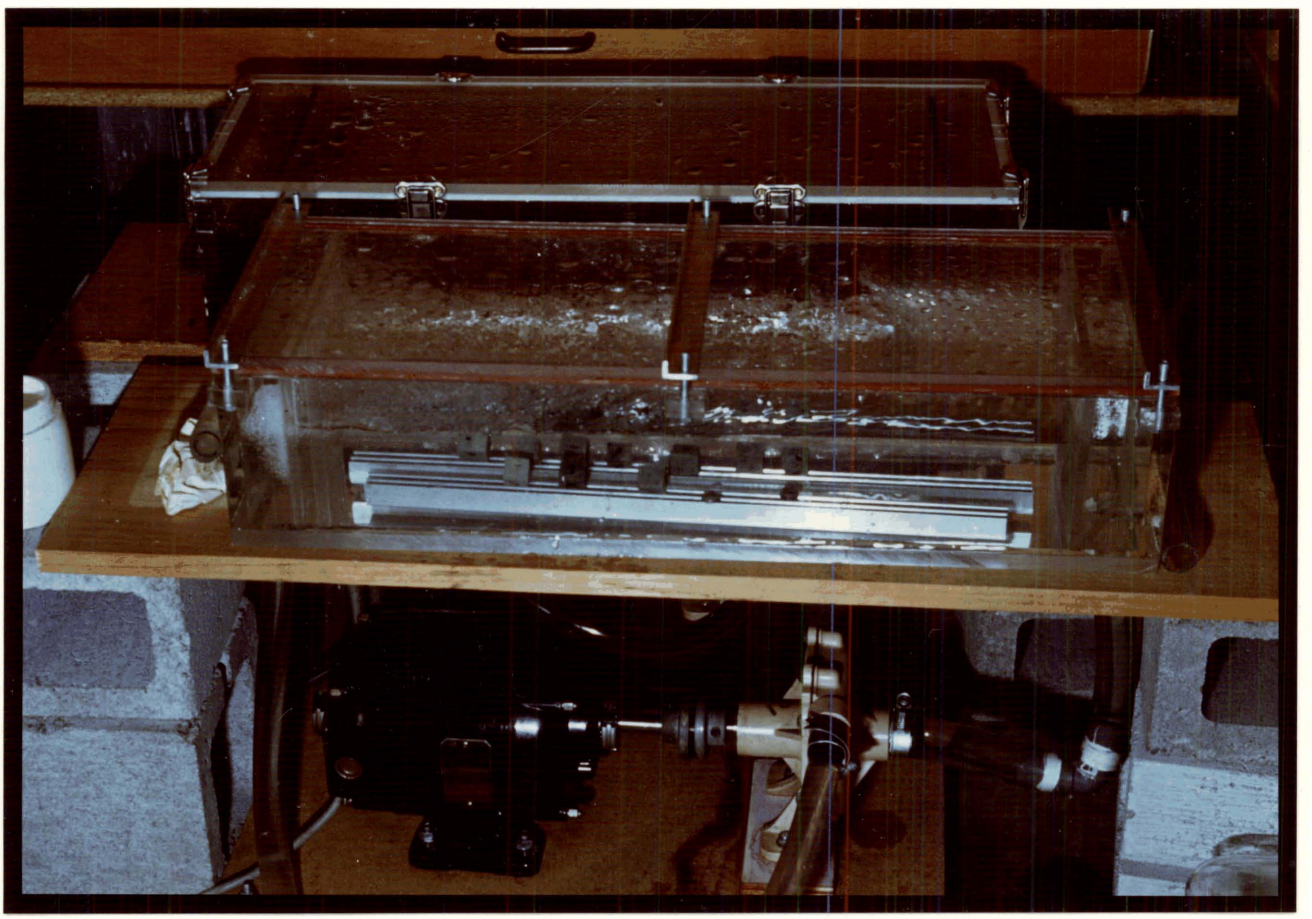
Experimental substrates were placed in the field channel at Middle Bush and covered by black polythene to prevent algal growth.

After 2, 4, 8, 12 and 16 weeks incubation (beginning 9 March 1980) 25 cubes and five chips were taken to the laboratory in containers of stream water. Nine cubes were placed in five flasks and oxygen uptake ($\mu\ell\ O_2.cm^{-2}.hr^{-1}$) was measured on a Gilson Differential Respirometer at a slow shaking speed (3) after a 2 hr equilibration period at ambient stream temperature.

Figure 3.1 The experimental channel at Middle Bush Stream showing incubating stones.

Figure 3.2 The spring site channel located against the spring vent.

Figure 3.3 The recirculating, experimental laboratory channels showing incubating stones.



Following this, cubes were placed in 250 ml Erlenmeyer flasks and oven-dried (60°C, 48 h). Total organic carbon (TOC) content of material adhering to cube surfaces was determined by the dichromate wet oxidation method of Maciolek (1962). The surface area of each cube was measured and both oxygen consumption and TOC levels calculated on an areal basis.

Twelve additional cubes were collected on each date for measurement of ATP. Cubes were placed in stainless steel centrifuge tube holders to which were added 16 ml of 0.2N Tris buffer and 0.5N $NaHCO_3$ premixed in a 2:3 ratio, and 4 ml $CHCl_3$. Tubes were capped with foil wrapped corks and manually shaken for two minutes to extract ATP from stone surfaces. Extracts were placed in 50 ml tubes and centrifuged for 10 min at 10,000 rpm. The supernatant (chloroform) was carefully pipetted off and disposed of while the remaining solution was frozen in the tubes until ATP determination was carried out.

ATP was determined on an ATP photometer (SAI Technology Co., Model 2000) using firefly enzyme (luciferase) (Sigma Chemical Co., St. Louis, U.S.A.). ATP salts were used to develop standard curves in the range 0.005 µg ATP.ml^{-1} to 1 µg ATP.ml^{-1}.

Chlorophyll *a* levels were determined on the other four cubes collected on each occasion. Cubes were soaked for 24 h in 30 ml of 90% acetone (made basic with several drops of $MgCO_3$) at 4°C and chlorophyll *a* was determined using the method of Wetzel & Westlake (1974).

Photographic documentation of the existence and development of the organic layer and its components was provided by scanning electron microscopy. On each sampling day, five stubs with chips attached were removed from the channels and fixed immediately in 5% gluteraldehyde in phosphate buffer. After 4 h, stubs were rinsed twice with buffer to prevent gluteraldehyde crystalisation and passed through an ethanol dilution series (30, 50, 70, 80, 90% once and 100% twice). Stubs remained in each solution for at least 0.5 h and were held in the second 100% solution overnight. They were critical point dried with liquid CO_2 after being infiltrated with amyl acetate, coated with approximately 15 nm of gold and viewed with a Cambridge Stereoscan 600 scanning electron microscope.

Layer Development in the Light and Dark

Cubes and chips were placed in the dark and under natural lighting regimes at both sites. ATP, organic carbon, chlorophyll *a* and oxygen

consumption were measured at 2, 4, 8 and 12 week intervals as described. Light input at the channel water surface was determined over a 24 h period on one occasion (21-22 March 1981) using the Ozalid paper integration method described by Rounick & Gregory (1981).

Leachate Uptake by Organic Layers

Radioisotopes were used to determine whether components of plant leachates were incorporated into the organic layer. Twenty-four graywacke cubes were incubated in the experimental channels for three months, by which time organic layers were well established.

Cubes were divided into three equal groups and treated as follows: Group 1 - soaked in concentrated chromic acid for 2 h to thoroughly clean the surface and then rinsed repeatedly with distilled water to remove the acid and any organic particles. Group 2 - placed in 3% formalin to stop all biological activity yet allow the layer to remain physically intact. Group 3 - kept in stream water at ambient stream temperature and not altered in any way.

Two series of experiments were run with the treated cubes, each using ^{14}C in a different form. In the first series *Elodea canadensis* was labelled with ^{14}C by placing apical sections of the plant in 1 litre Erlenmeyer flasks containing 500 ml of Chu Number 10 growth medium (Chu, 1942) to which had been added 50 µCi of ^{14}C in the form of $NaHCO_3$. The flask was placed in a sunlit window for 48 h to obtain sufficient and uniform labelling of the plant. *E. canadensis* was then removed from the flask, rinsed in double distilled water and oven-dried for 24 h before being ground to a fine powder with a mortar and pestle. Powder was leached in a small volume of autoclaved stream water under sterile conditions and filtered. The radioactivity of an aliquot of leachate produced in this way was determined and further aliquots added to treated stones (five of each type) in bowls of autoclaved stream water at about 10 µCi.100 ml^{-1}.

^{14}C in the form of protein hydrolysate (Radiochemical Centre, Amersham, U.K.), a mixture of 16 amino acids in varying concentrations, also was used to simulate organic constituents of leachates which might be available to the microflora of a forested stream. Hydrolysate was added to a second series of 15 cubes.

All containers were placed on a gently shaking table at 12°C (approximately ambient stream temperature) and incubated for 2, 5, 8 and

15 h. Upon removal, stones were rinsed gently in distilled water and carbon adhering to stone surfaces was digested in a 1:2 mixture of 60% perchloric acid and hydrogen peroxide (Mahin & Lofberg, 1970). One ml of digestant was added to 14 ml of scintillation cocktail, dark adapted and counted on a Nuclear-Chicago Unilux III Liquid Scintillation Counter using the channels ratio method.

Leachate: Microbial Respiration Experiments

The effect of leaf leachates on rates of oxygen consumption by surface-colonising micro-organisms was examined in a series of leachate addition experiments. Fresh leachate was made by soaking approximately 50 g of mountain beech leaves in 10 ℓ of distilled water with occasional stirring. After 24 h the leachate was filtered (0.45 μm), freeze-dried and stored.

Dead mountain beech leaves incubated in Middle Bush Stream for ten weeks were used as microbially colonised substrates. About 7 g dry weight of leaves were added to trays containing 500 ml of stream water and leachate was added to one tray to bring the concentration of dissolved organic carbon to 40 $g.m^{-3}$. Both trays were kept at 5°C and aerated continuously.

Respiration rates of five replicate leaf samples (each about 250 mg dry weight) from each tray were measured at the start of the experiment and after 24, 48, 72, 96 and 120 h using a Gilson Differential Respirometer.

Organic Layer Formation in Laboratory Channels

Two laboratory experiments were set up to examine the role of leaf leachate in the formation of the organic layer. In the first experiment graywacke cubes and chips were incubated for four weeks at 6°C ± 1.5°C in the dark in two 12 ℓ pump-driven recirculating experimental channels (Figure 3.3). Each channel contained just under 12 ℓ of distilled water to which was added 500 ml of Middle Bush Stream water to seed the channels with micro-organisms. An 0.5 mm mesh leaf bag containing 50 g dry weight of mountain beech leaves was placed in one channel for five days and then removed. Dissolved organic matter (DOM) from this material served as the available organic carbon source and brought DOC levels up to a maximum of 100 $g.m^{-3}$. No leaf bag was added to the second channel.

Chips and cubes were removed weekly for four weeks and used to measure ATP (six cubes), total organic carbon (five cubes) and oxygen

consumption rates (seven cubes). Chip surfaces were examined with the scanning electron microscope. On every sampling date, eight aliquots of water were taken from each channel for measurement of organic carbon. Samples were filtered (0.45 µm) to separate DOC from particulate organic carbon (POC) and both were measured by wet oxidation (Maciolek, 1962). Water column pH was monitored weekly using a Metrohm Herisau pH meter.

In a second experiment, leachates were introduced to both channels to bring DOC levels to a maximum of 50 $g.m^{-3}$ and concentrated formalin was added to one channel to achieve a final concentration of 3%. Samples were collected on a more intensive basis than in the first experiment; at 8-12 h intervals for the first seven days and then at one and three day intervals until day 23. On day 25 a new bag of leaves was placed in each channel as a source of additional leachate. The response to this leachate pulse was monitored daily for five further days. Oxygen consumption was not measured in this experiment.

Utilisation of the Organic Layer by Invertebrates

A dual-label radiotracer technique based on that described by Calow & Fletcher (1972) was used to measure assimilation efficiencies and feeding rates of some beech forest stream invertebrates on stone surface organic layers. ^{14}C was used as the absorbed radioisotope while ^{144}Ce was used as the non-absorbed indicator. The suitability of ^{144}Ce in this respect was checked by counting radioactivity in bodies of ten *Deleatidium* (mayfly) larvae and in faeces, following 12 h feeding on labelled food and a 12 h gut clearance time. Body counts were less than 2.5% of those in faeces and even then could have been contributed to by incomplete gut clearance.

All animals were collected in the Cass area and taken to the laboratory within 4 h. There they were kept in trays of aerated stream water at ambient stream temperature for up to 24 h before being used in experiments.

Graywacke slabs, incubated in the dark in the Middle Bush experimental channels for three months, and stones from different streams with variously developed periphyton coatings were offered as foods. The latter were taken from three streams and their algal coatings were designated as: (1) High density - primarily filamentous green algae; (2) Medium density - mainly filamentous diatoms and some filamentous greens; (3) Low density - solitary diatoms only in low numbers. Densities were quantified by measuring chlorophyll *a* levels.

Stones were labelled with a combination of D-(U-^{14}C) glucose and/or sodium (^{14}C) bicarbonate at concentrations of 10 µCi.100 ml^{-1} by placing stones and slabs into plastic containers with stream water for 4 h. Cerium as ^{144}CeCl was then added at a concentration of 10 µCi.100 ml^{-1}.

Algal-colonised stones were labelled with ^{14}C-bicarbonate, ^{14}C-glucose or both. Bicarbonate was used so the label would be incorporated principally by algal cells whereas glucose (^{14}C) should be taken up only by bacteria and fungi. To ensure that sufficient label had been incorporated, the specific activity of each food type was checked two hours after the addition of the ^{144}Ce label.

Feeding rates (ingestion rates) of invertebrates were determined indirectly by measuring levels of ^{144}Ce in faeces and relating these to the known radioactivity per unit weight of food. Assimilation efficiencies were determined by comparing ratios of ^{14}C and ^{144}Ce in food and faeces as developed by Calow & Fletcher (1972).

The number of animals of each species necessary to produce sufficient faecal material for analysis ranged from 1 to 10. Animals and foods were placed in water-filled containers consisting of a plastic pottle with a 1 mm mesh floor inserted inside a second unmodified pottle. Animals could thus feed freely but were prevented from ingesting faecal material which fell through the mesh floor.

Animals were allowed to feed for up to 24 h when labelled food was removed and the mesh-floored container of experimental animals was inserted in a second outer pottle containing fresh water and unlabelled food. The level of radioactivity of the faeces was always highest in the first faecal collection after removal of the labelled food. This is similar to Greig's findings (1976). Faeces produced in the first four hours following this transfer were collected on 0.45 µm filters and used to calculate feeding rates (see Greig, 1976). A check on the radioactivity of water above faeces and experimental animals in feeding containers revealed only minor activity, <2% of that measured in the faeces, indicating little leaching of isotopes from foods or faeces. Upon completion of experiments invertebrates were dried and weighed.

Samples of food and faeces were digested using the procedure of Mahin & Lofberg (1970), placed in borosilicate vials with 15 ml of scintillation fluid, and dark-adapted for 12 h. After calibration of the scintillation counter to maximise β energy separation vials were counted using the external standard ratio technique. This allowed counting

efficiencies from differently quenched samples to be determined and enabled the net activity of ^{14}C and ^{144}Ce to be calculated (Hendee, 1973). Assimilation efficiency was calculated from the formula:

$$\text{Assimilation efficiency} = 1 - \frac{\text{cpm } ^{144}\text{Ce(food)}/\text{cpm } ^{14}\text{C(food)}}{\text{cpm } ^{144}\text{Ce(faeces)}/\text{cpm } ^{14}\text{C(faeces)}} 100$$

RESULTS

Layer Development in the Dark

The structure and biological activity of the developing organic layer in the dark, Middle Bush Stream channel is shown in Figures 3.4 and 3.5. Organic carbon built up rapidly in the first month but increased only slightly in month 2 to a level ($\simeq 0.08$ mg.cm^{-2}) which was maintained in the subsequent two months of the experiment. In contrast, ATP and oxygen consumption rates had their greatest increases in month 2 before levelling off. Chlorophyll *a* was undetectable throughout, and indicated there was little autotrophic production in the channel.

The scanning electron micrographs successfully complemented the chemical data. A bare rock surface before incubation is shown in Figure 3.5a. After one month small detrital fragments and loose patches of slime (5-20 µm across) were present on the stone surface and small groups of bacterial rods and cocci were visible (Figure 3.5b). After two months the slime layer was almost continuous and fungal hyphae were abundant. Some diatom frustrules which must have drifted into the channel also occurred.

Fungi may have been primarily responsible for the large increase in ATP and oxygen consumption rates observed between months one and two. The three and four month micrographs (Figure 3.5c) indicate stabilisation of the layer structure. Stone surfaces were completely covered with slime, and bacteria (generally associated with the slime), fungal hyphae, diatom frustrules and trapped fine particles can be seen. The thickness of the layer at this time was estimated to be about 80 µm.

Layer Development in the Dark and Under Natural Lighting at Contrasting Sites

Marked differences in all measured parameters were found between the two sites (Middle Bush Stream and the spring) and between layers formed in the light and dark.

Figure 3.4 Levels of organic carbon, ATP and oxygen consumption recorded in four months from substrates incubated in the dark experimental channel at Middle Bush Stream. Vertical bars represent 1SE of the mean.

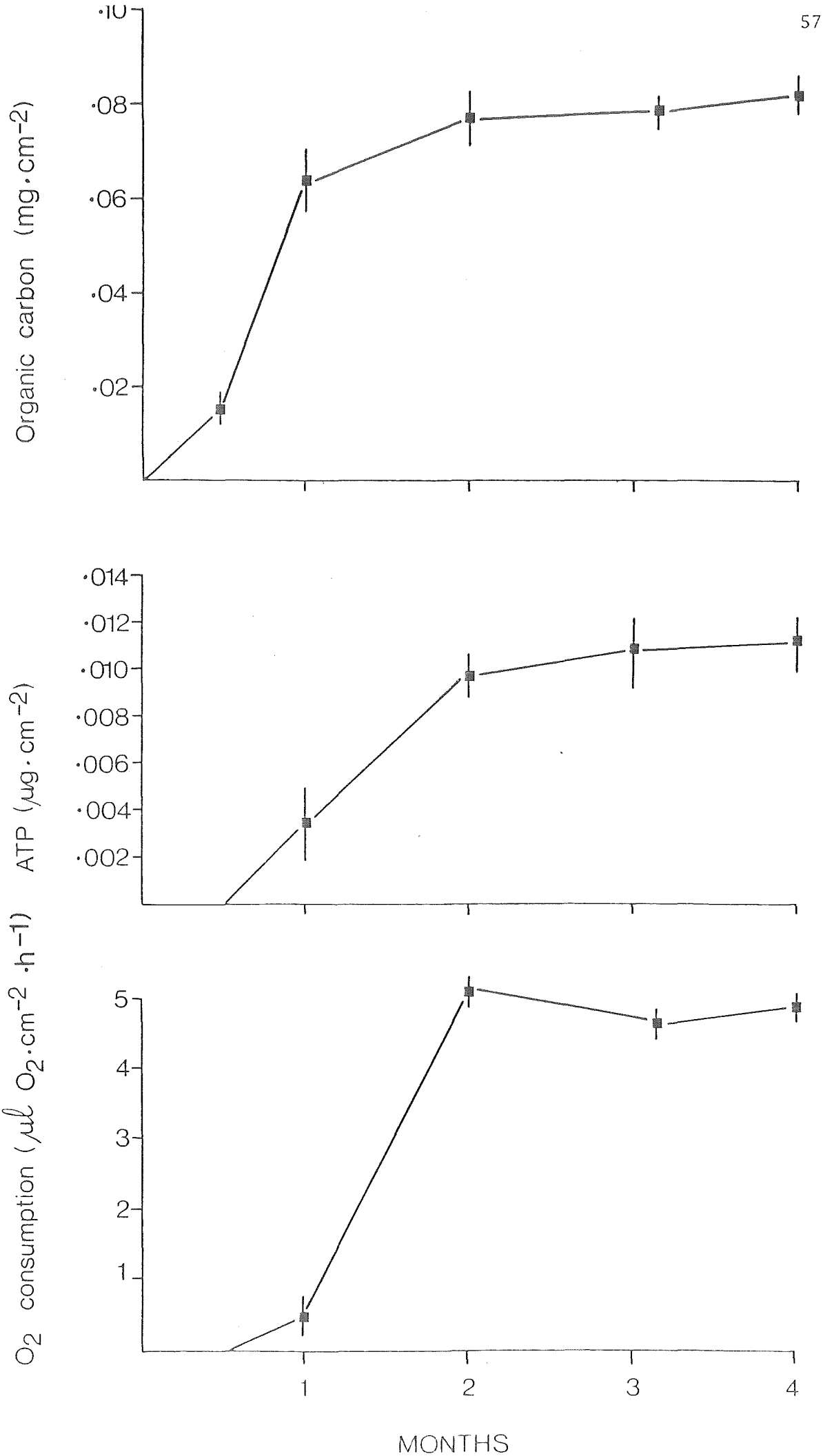
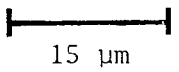
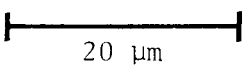

·10
·08
·06
·04
·02
Organic carbon (mg·cm⁻²)
·014
·012
·010
·008
·006
·004
·002
ATP (µg·cm⁻²)
5
4
3
2
1
O₂ consumption (µl O₂·cm⁻²·h⁻¹)
1
2
3
4
MONTHS

Figure 3.5 Organic layer development in the darkened Middle Bush channel.

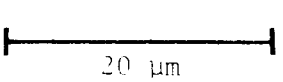
(a) Clean, day 0.

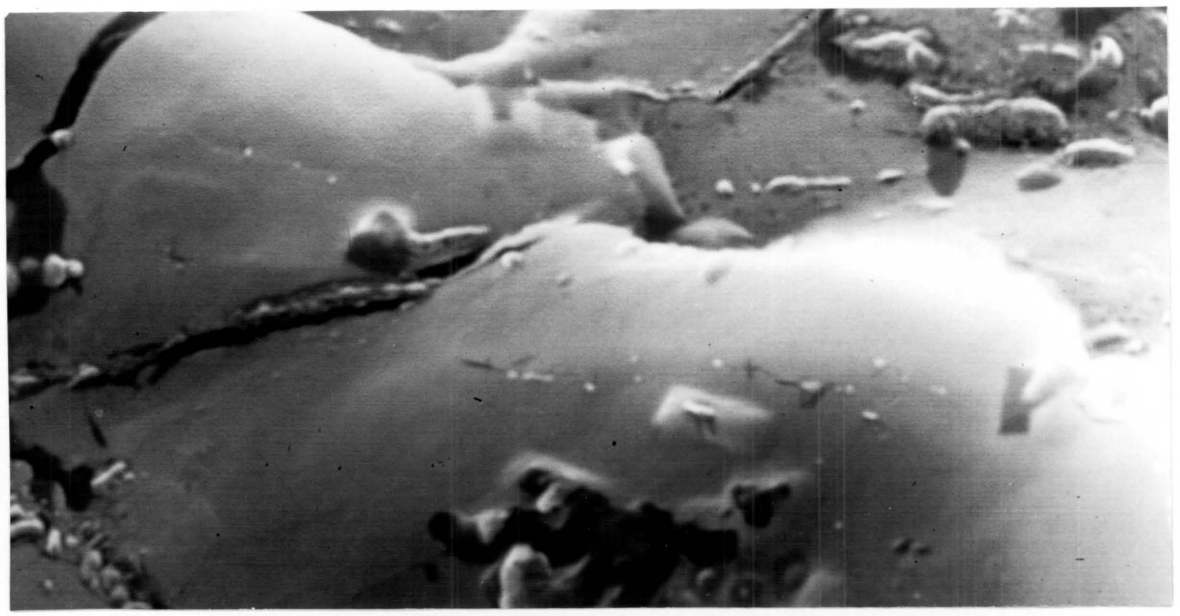


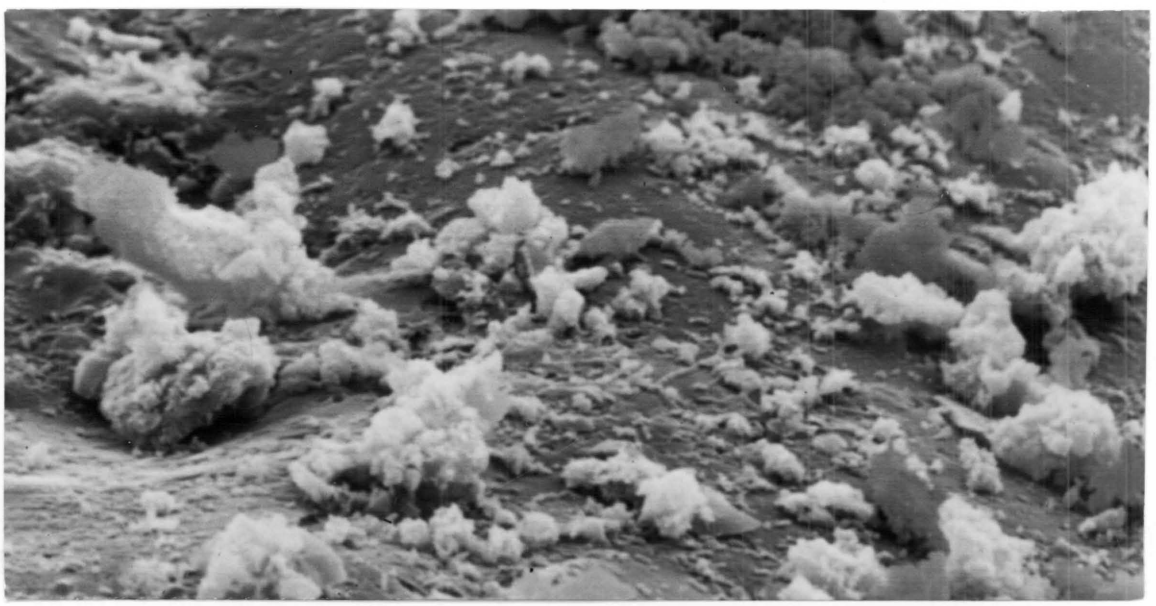
(b) After one month showing scattered slime, fine particles and bacterial cells.



(c) After three months showing a continuous slime layer with embedded particles (e.g., upper left), fungal hyphae and diatom frustrule.







Organic layer development in the dark Middle Bush channel was similar to that described above with respect to the parameters measured (Figure 3.6). This was despite the experiment being carried out from January - March (cf. March - July for the initial Middle Bush experiment).

Stones incubated under a natural light regime at Middle Bush Stream also were colonised by abundant algae, in particular the diatoms, *Rhoicosphenia* and *Cocconeis* (Figure 3.7a). Filamentous algae were absent however, probably because light intensities were low (values recorded over a 24 h period: Middle Bush Stream - 14 langley.day^{-1}; spring site - 58 langley.day^{-1}). Oxygen consumption rates and ATP levels at Middle Bush Stream were similar recorded from stones in the open spring site channel despite the presence of quite different algal communities (see below) and algal biomass as indicated by chlorophyll *a* levels (Figure 3.6). This suggested that the heterotrophic components of the organic layer were more strongly developed at Middle Bush Stream.

Stones incubated under natural lighting at the spring site became heavily colonised with filamentous green algae and diatoms within one month of incubation (Figure 3.7b). Maximum chlorophyll *a* levels observed were comparable to those given by Eloranta & Kunnas (1979) for an open Finnish river and six times higher than those reported for a large turbid northern Canadian river by Barton & Lock (1979). Populations of bacteria with thread-like attachment fibres were observed colonising intercellular areas of filamentous diatoms where leakage of organic materials may occur (Figure 3.7c). Some slime appeared to be associated with these bacteria but, because of the thickness of the algal mat, it could not be determined whether slimes and bacteria were associated with the stone surface. Few fine detrital particles were observed. Chlorophyll *a*, oxygen consumption, organic carbon and ATP were all highest at this site and continued to rise throughout the 3-month period (Figure 3.6).

Scanning electron micrographs of stones incubated in the dark at the spring site, showed that most of their surfaces were bare (Figure 3.7d). This is in direct contrast to the situation found in Middle Bush Stream where a relatively thick and biologically active layer formed in the dark. Levels of DOC measured in water samples from the two sites were very different (<0.5 g.m^{-3} - spring site; 5 g.m^{-3} - Middle Bush Stream). The very low levels of DOC (and nitrogen; unpublished data) and the absence of particulate inputs almost certainly explain this difference.

Figure 3.6 Detectable levels of organic carbon, ATP, oxygen consumption and chlorophyll *a* recorded in three months from substrates incubated in light (□) and dark (■) channels at Middle Bush Stream (left) and the spring site (right). Vertical bars represent 1SE of the mean when >5% of the mean.

MIDDLE BUSH STREAM

SPRING SITE

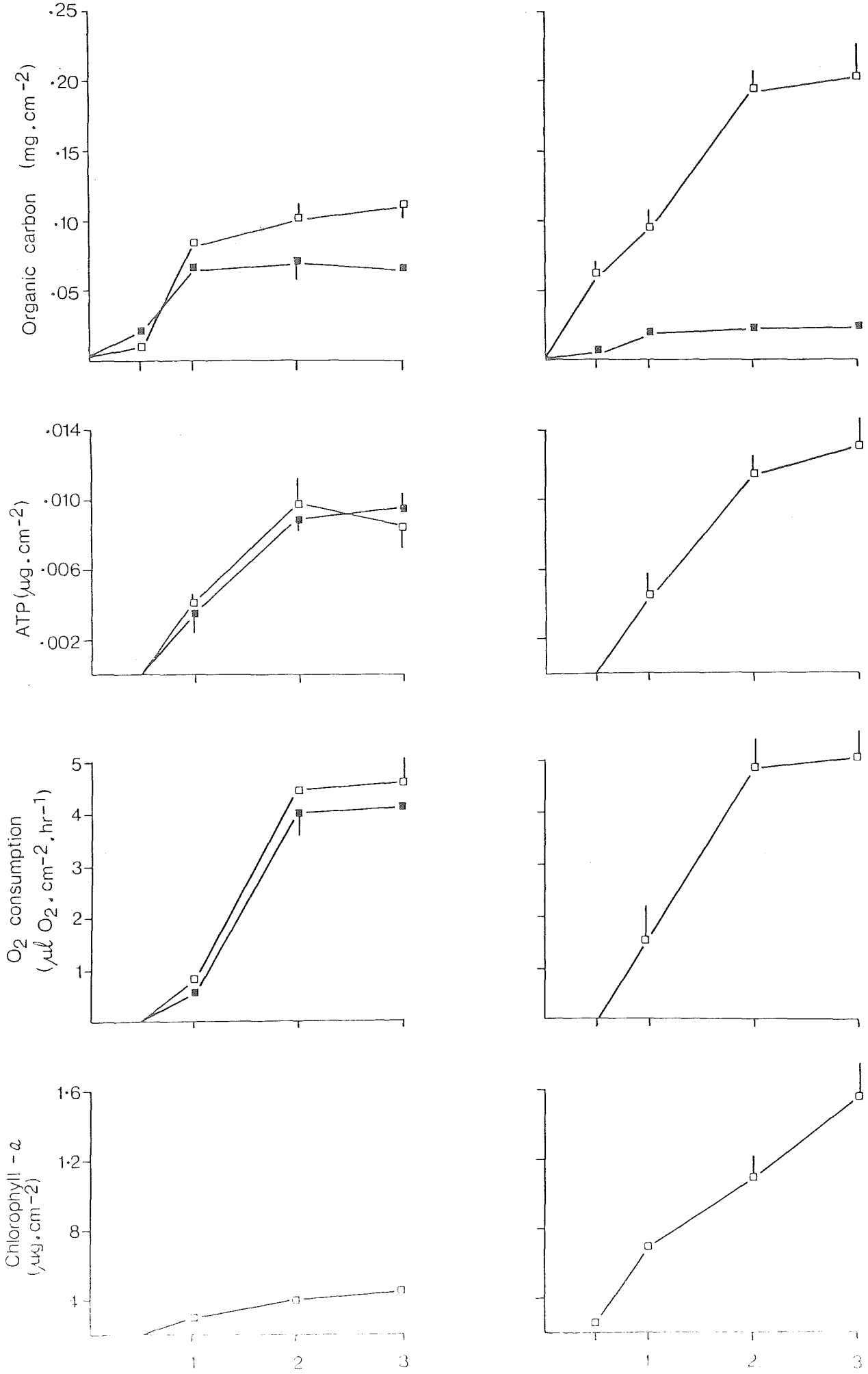
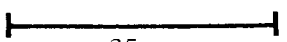


Figure 3.7 Organic layer development on stone surfaces in dark and light field channels.

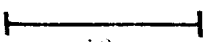
(a) Middle Bush light after two months, *Cocconeis* prevalent. White structures may be protozoan cysts.

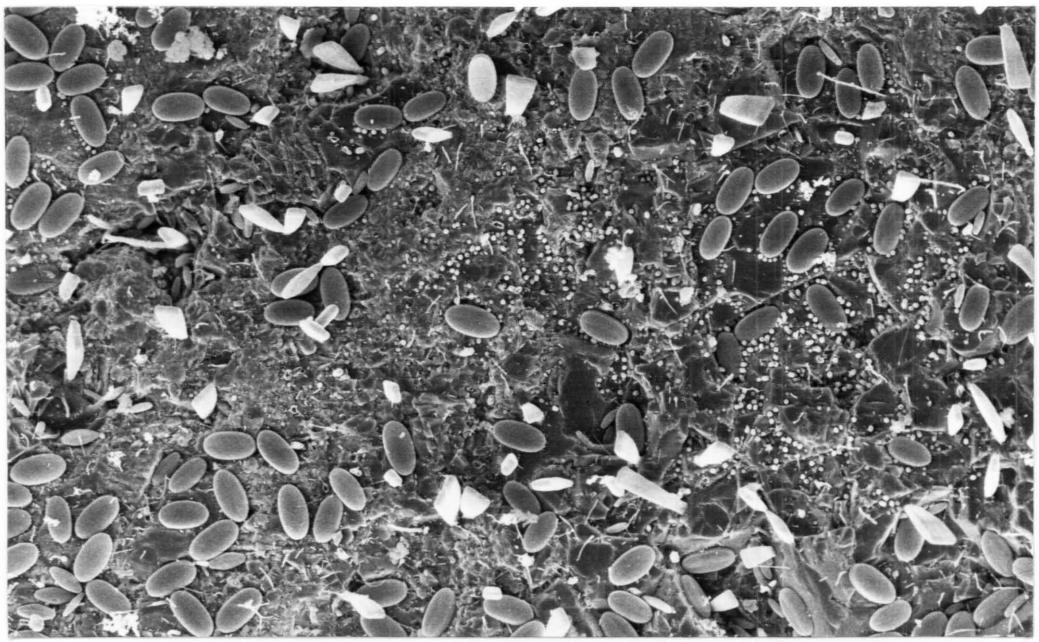
(b) (left) Spring site light after one month showing well developed algal filaments. Note picture quality is poor because of thickness of the layer and charging of the loose filaments.

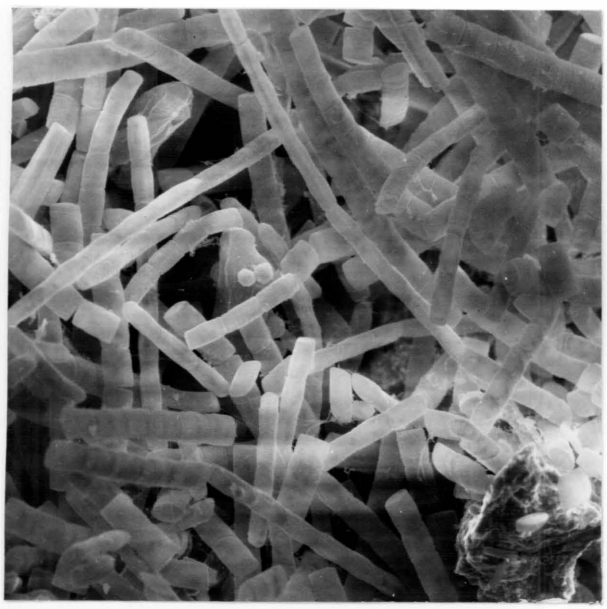
(c) (right) Spring site light. Bacteria attached with thread-like projections to algal filaments (*Melosira* sp.). Note bacteria may be associated with sites of nutrient leakage from the alga.

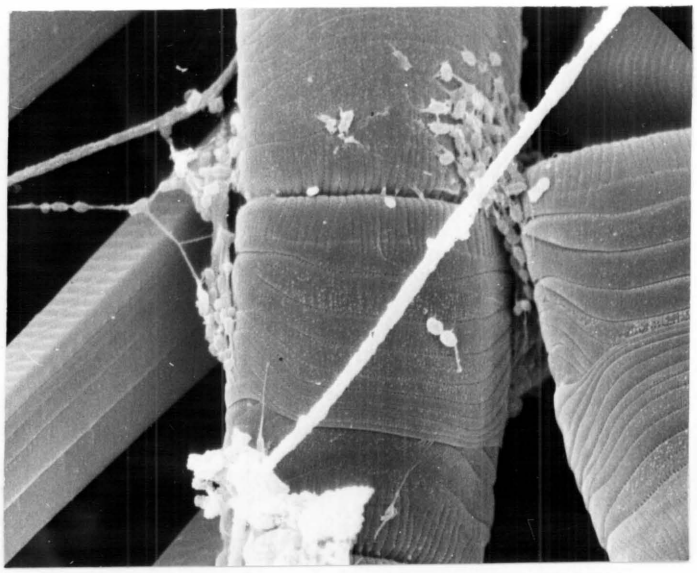


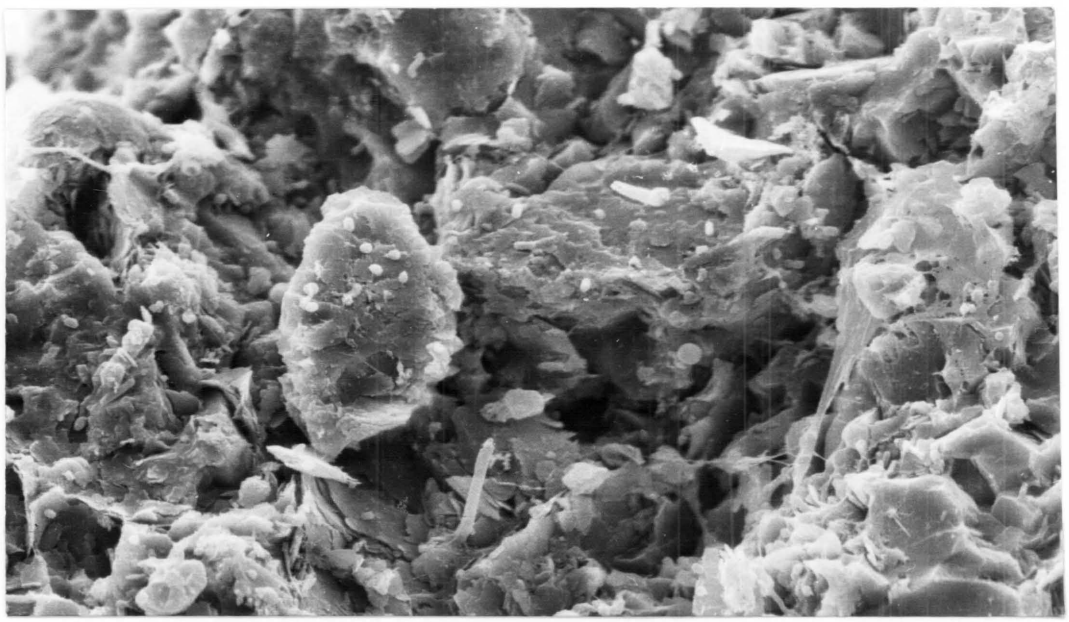
(d) Spring site dark after three months, no evidence of organic layer formation, however, scattered bacterial cells can be seen.











Leachate Uptake Experiments

Experiments with ^{14}C-labelled protein hydrolysate and radioactive *Elodea* leachate demonstrated that it was taken up by both biotic and abiotic means. Acid-washed stones and stones with intact layers treated with 3% formalin accumulated radioactive carbon throughout each 15 h experiment (Figure 3.8). However, much greater and more rapid initial uptake of ^{14}C occurred on stones with intact "living" organic layers and final levels were up to three times greater than on the other surfaces.

Experiments were discontinued after 15 h because it was hard to keep acid-washed stones relatively microbe free after this time.

Effects of Leachate Additions on Respiration of Colonising Micro-organisms

In the first 48 h after the addition of mountain beech leachate, only small (not significant) differences in respiration rates were found between leaves with and without leachate additions (Figure 3.9). However, after 72 h an approximate 65% increase was observed in leachate-added leaves; a further small increase occurred at 96 and 120 h. Control leaves showed no increases at these times indicating that microbial metabolism and/or growth was stimulated by leachate additions.

Organic Layer Formation in the Laboratory

Experiment 1. Experiments were carried out in two recirculating channels. In the channel with no added leachate, little or no organic layer development occurred on stones and neither ATP nor microbial respiration were detectable (Figure 3.10). Micrographs of stone surfaces showed only slight accumulations of organic matter after 2-3 months incubation and stones looked similar to those incubated in the dark portion of the spring site channel.

Stones in the channel to which leachate had been introduced developed a complex, biologically active organic layer resembling somewhat that found in the dark in the Middle Bush channel. Results of the weekly assays of pH, DOC and POC in the water column, and oxygen consumption, ATP and organic carbon on stone surfaces are shown in Figure 3.10. DOC levels in the water column increased from about 3 $g.m^{-3}$ to 100 $g.m^{-3}$ in the first week as leaching of litter in mesh bags proceeded. Concurrently, pH decreased from 6.0 to 4.8 as fulvic acid and other acidic components of leachate were released. DOC levels subsequently declined as a result of uptake on surfaces in the channel and pH increased again almost to its

Figure 3.8 Accumulation of radioactive Carbon-14 on stone surface organic layers under the following treatments: ▲ - chromic acid washed, □ - formalin washed, ■ - untreated. (a) ^{14}C added as protein hydrolysate, (b) ^{14}C added as *Elodea canadensis* leachate. Vertical bars represent 1SE of the mean when >5% of the mean.

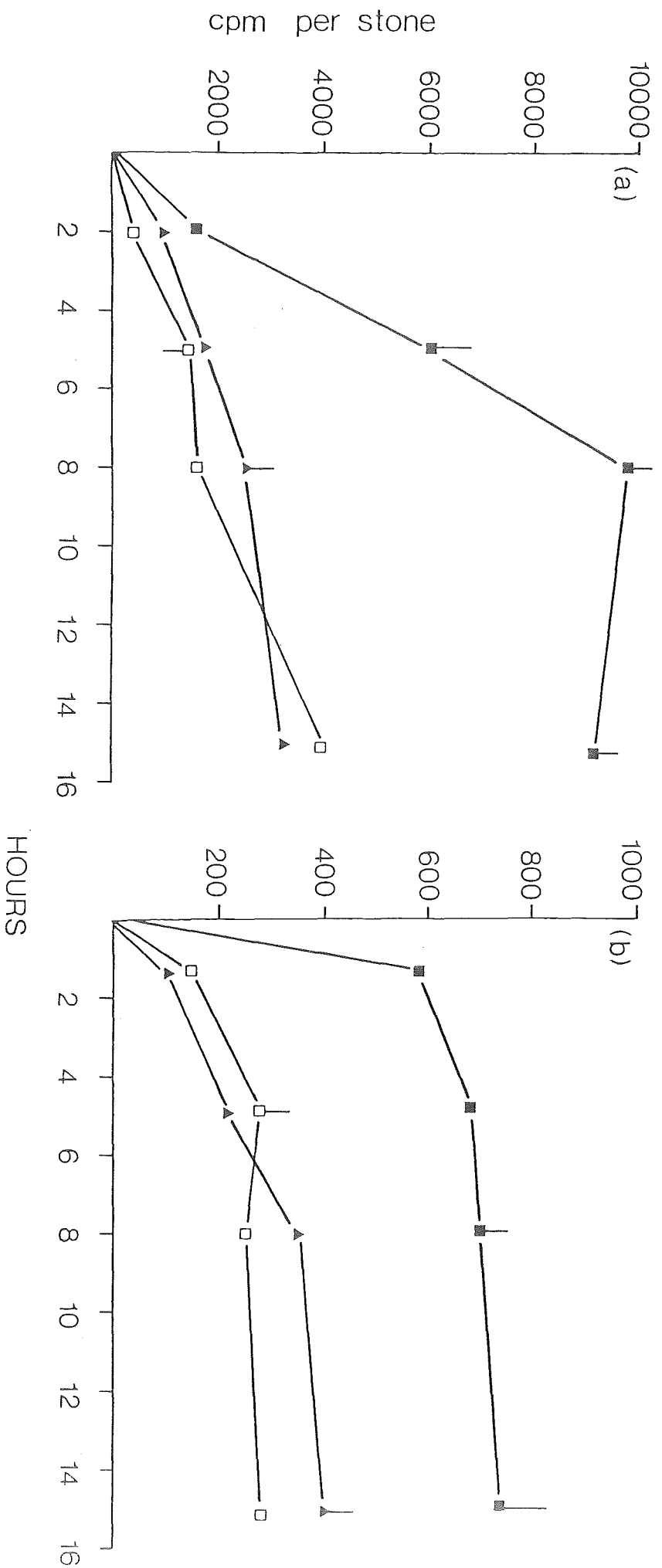

cpm per stone
2000
4000
6000
8000
10000
(a)
200
400
600
800
1000
(b)
2
4
6
8
10
12
14
16
HOURS

Figure 3.9 Effect of beech leachate introduction on the rate of oxygen consumption of decomposing mountain beech leaves over 120 h. □ - control (no leachate added), ■ - leachate introduced. Vertical bars represent 1SE.

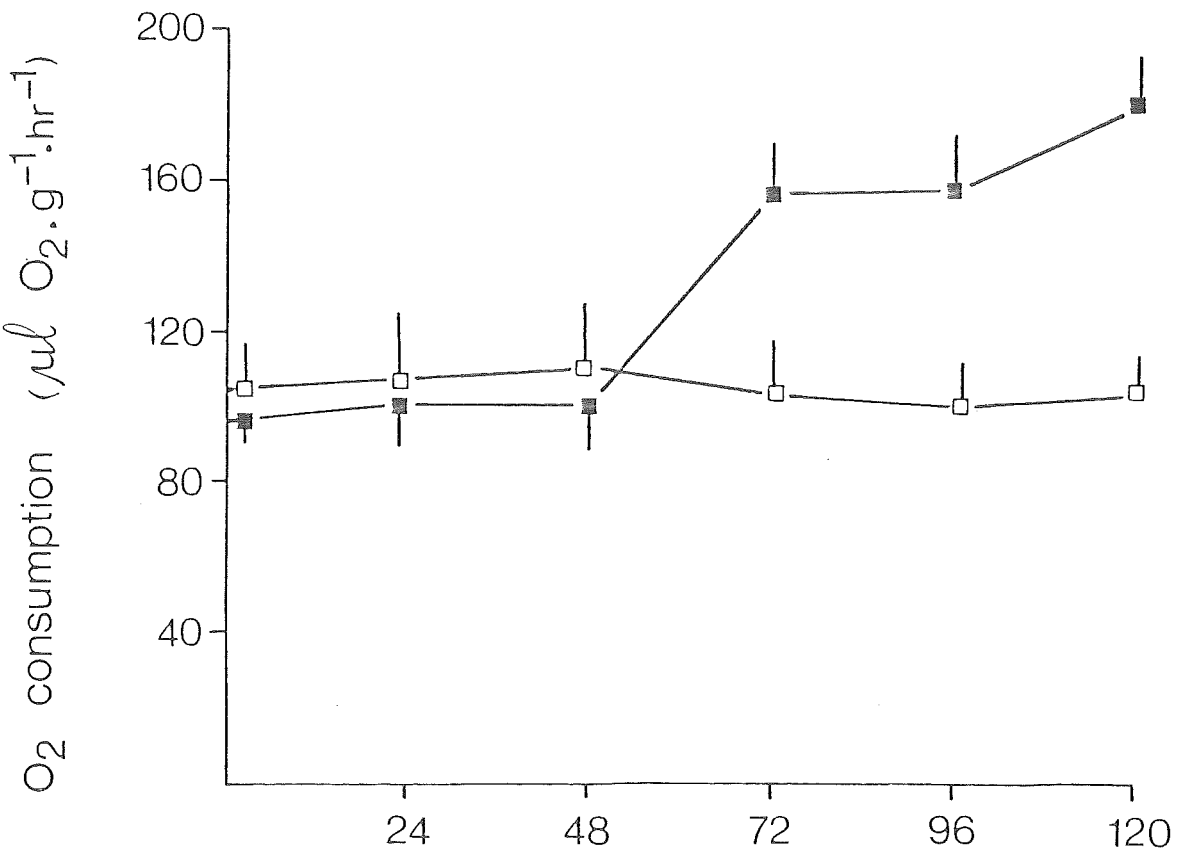
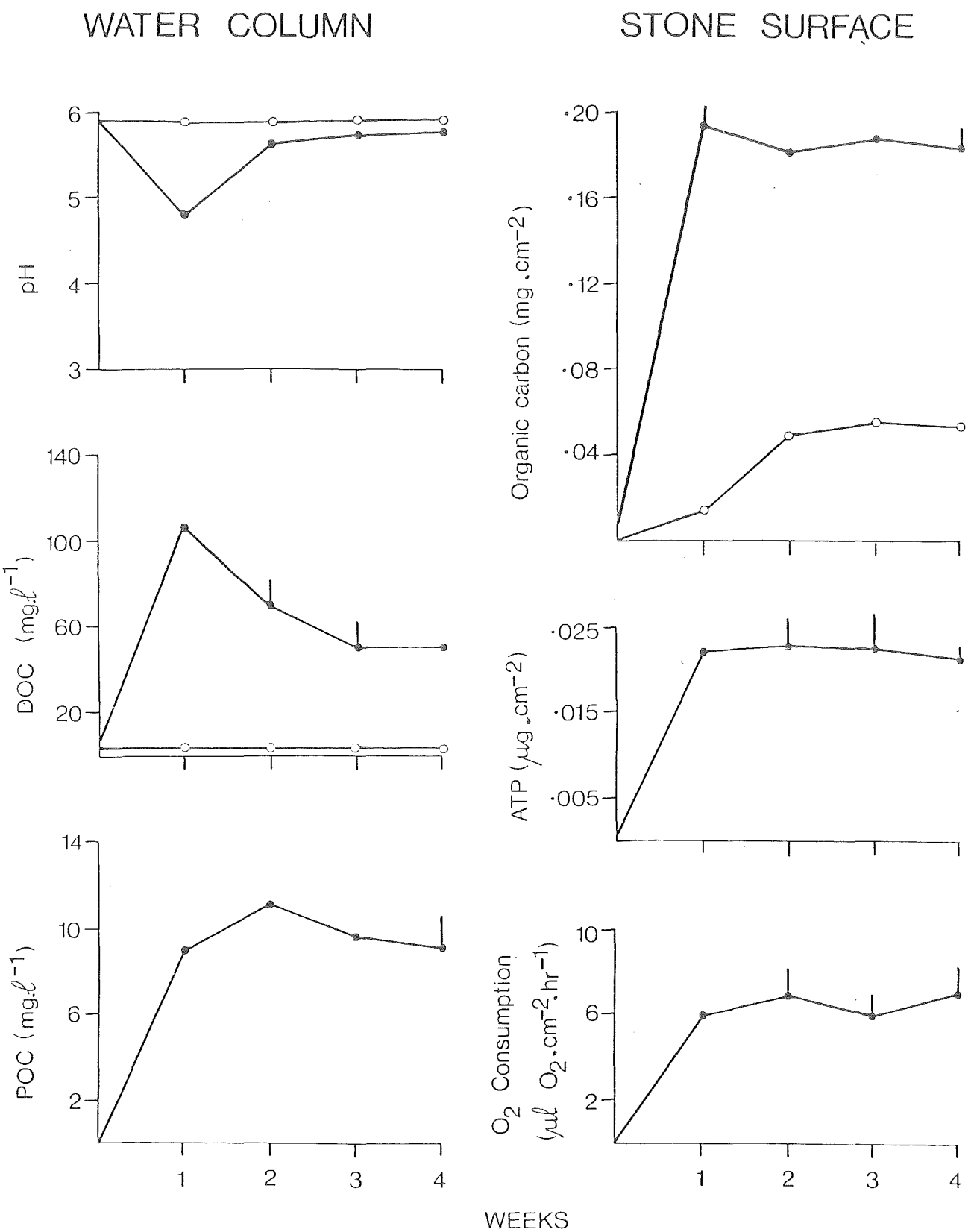

200
160
120
80
40
24
48
72
96
120
O2 consumption (µl O2.g-1.hr-1)

Figure 3.10 Detectable levels of water column pH, DOC and POC (left) and stone surface organic carbon, ATP and oxygen consumption (right) recorded in the recirculating laboratory channels. O - no leachate channel, ● - leachate channel. Vertical bars represent 1SE of the mean when >5% of the mean.


WATER COLUMN
STONE SURFACE
pH
6
5
4
3
DOC (mg.ℓ⁻¹)
140
100
60
20
POC (mg.ℓ⁻¹)
14
10
6
2
Organic carbon (mg.cm⁻²)
·20
·16
·12
·08
·04
ATP (μg.cm⁻²)
·025
·015
·005
O2 Consumption (μl O2.cm⁻².hr⁻¹)
10
6
2
1
2
3
4
WEEKS

initial level. Like DOC, water column POC showed a marked increase in week 1 but, unlike DOC, remained elevated throughout the remainder of the experiment. This indicated that bacteria and/or fine detrital particles were present in the water column at all times.

Stone surface respiration, ATP and organic carbon increased sharply in the first week and levels attained at that time were maintained throughout the four-week experimental period.

Micrographs demonstrated that almost all stone colonisation occurred within the first seven days after leachate introduction (Figure 3.11 a, b). Dense mats (200-400 μm thick) of fungal hyphae and associated bacteria developed in the first week of the experiment and after seven days, but not thereafter, ciliated protozoans were observed within the mats (Figure 3.11c).

In the first week, large amounts of rather amorphous material ("slush") also accumulated on the mesh baffles within the channel. Under the light microscope, "slush" resembled the material which occurred on the stones and included bacteria, protozoans, fungal hyphae and a large mass of amorphous particulate material. The origin of this material is unclear since the channels were virtually particle free at the start of the experiment and leaves had been carefully washed prior to being placed in mesh bags. Therefore, it is presumed they were formed during the experiment from leaf leachates. Stable carbon isotope analysis demonstrated they had somewhat enriched $^{13}C/^{12}C$ ratios relative to beech leachate ("slush" - 23.8 per mille; beech leachate - 25.3 per mille, unpublished data), which suggests microbial mediation during slush formation (McConnaughey & McRoy, 1979).

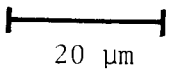
Experiment 2. This experiment was run to investigate in more detail the initial period of rapid layer development observed in experiment 1, and to examine the effects of a further leachate addition following the establishment of the layer (after 25 days). Formalin and leachate were added to one channel whereas leachate only was added to the other.

Large differences were found between the channels (Figure 3.12). No organic layer developed in the formalin-treated channel although some organic carbon was detected on stone surfaces. DOC levels remained at $\simeq$ 50 $g.m^{-3}$ throughout the experiment indicating that little if any abiotic uptake of DOM occurred. pH levels remained low throughout owing to the presence of acidic leachate components and formic acid.

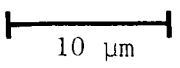
A dense organic layer similar to that which developed in experiment 1 formed in the second channel. Water column DOC levels were lower however,

Figure 3.11 Organic layer development in recirculating laboratory channels.

(a) After one week organic layer development in the leachate channel (Experiment 1). Fungal hyphae, bacteria and associated slime are abundant.



(b) Close-up of (a) showing relationship between fungal hyphae and slime.



(c) A layer inhabiting ciliate found between days 5 and 10 in Experiment 2.

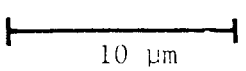
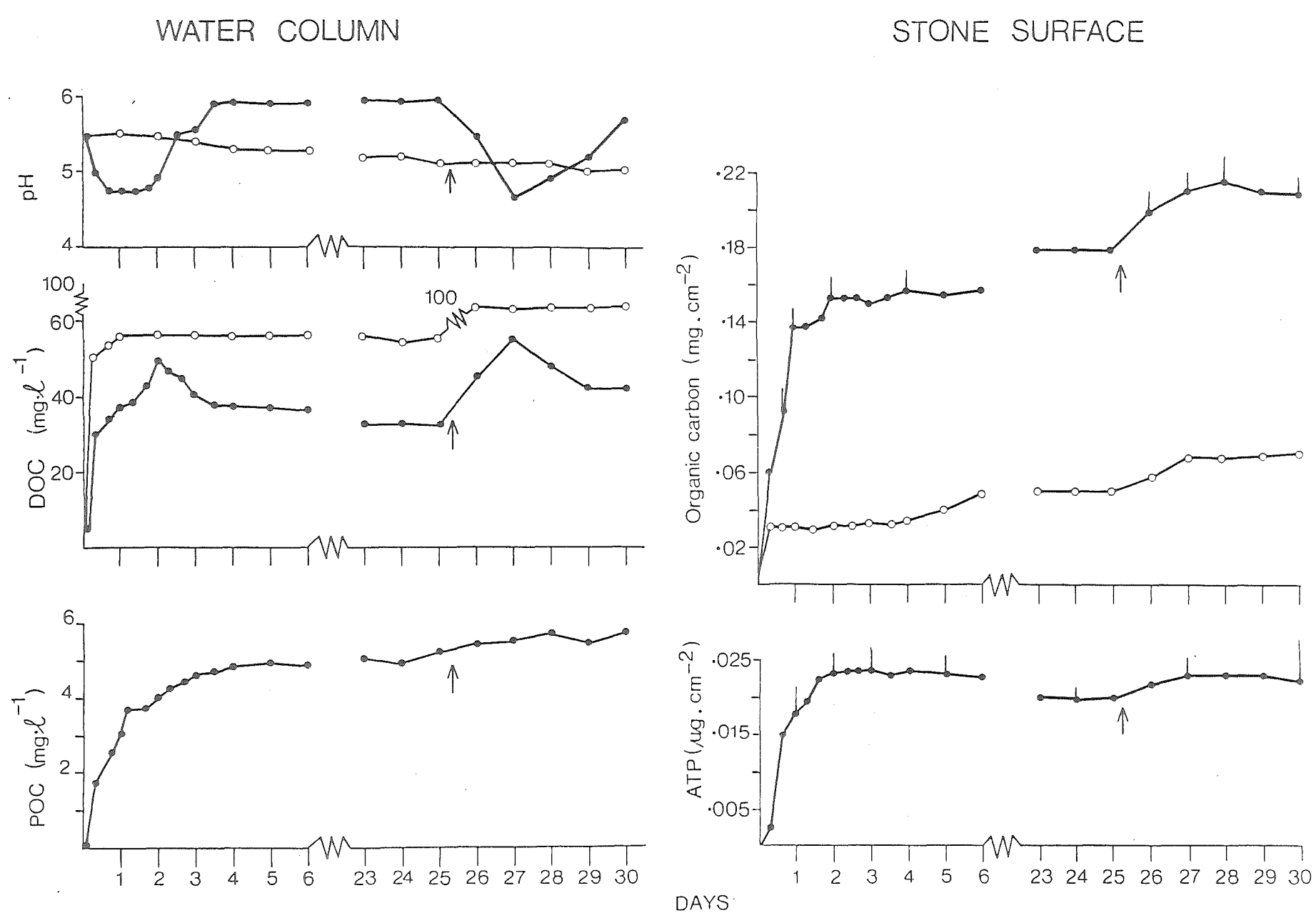


Figure 3.12 Detectable levels of water column pH, DOC and POC (left), and stone surface organic carbon and ATP (right) recorded in recirculating experimental laboratory channels during Experiment 2. ● - biologically active channel, ○ - formalin treated channel. The arrow demarcates the time of the second leachate addition to the channels (after 25 days). Vertical bars represent 1SE of the mean when >5% of the mean.


WATER COLUMN
STONE SURFACE
pH
6
5
4
DOC (mg·ℓ⁻¹)
100
60
40
20
100
POC (mg·ℓ⁻¹)
6
4
2
Organic carbon (mg.cm⁻²)
·22
·18
·14
·10
·06
·02
ATP (µg.cm⁻²)
·025
·015
·005
1 2 3 4 5 6 23 24 25 26 27 28 29 30
DAYS

because fewer leaves were used to produce the initial leachate. This lower leachate introduction also may have been responsible for the more rapid attainment of maximum water column DOC, POC and pH levels than in experiment 1.

Micrographs showed that slime and bacterial colonisation occurred together within 4 h of leachate introduction and increased rapidly after 8 h so that about 80% of the stone surface was covered in 16 h. After 24 h, bacterial rods were prevalent in most microscope fields and the layer had a fuzzy appearance given by the slime balls which were closely associated with bacteria suggesting that the slime was a bacterial secretion. After two days, fungal hyphae began to appear and were the dominant organisms on day 5. At this time, large colonies of "slime" bacteria were seen along with ciliated protozoans which had disappeared by day 10 (Figure 3.11c). "Slush" also formed in the biologically active channel four days after the introduction of leachate.

On day 25, a pulse of fresh leachate was added to the channels by introducing a new mesh bag of leaves. Data for the two days prior to the leachate pulse and the five days thereafter are shown in Figure 3.12 Both stone surface and water column indicators responded to this second input in a similar fashion to the first pulse except that increases were not as marked. After the leachate pulse, the organic layer became larger as evidenced by increased stone organic carbon levels and the biological components somewhat denser as seen on electron micrographs.

The Organic Layer as a Food Source for Invertebrates

Stones with surface organic layers grown in the dark Middle Bush channel (i.e., lacking algae) were offered to eight common invertebrates in 24 h feeding experiments. The two primarily predatory insects, *Stenoperla prasina* and *Philorheithrus agilis*, produced no radioactive faeces whereas all other species ingested organic layer material at rates ranging from 2.5 to 6.8 µg dry weight.mg body dry weight^{-1}.h^{-1} (Table 3.1) Calculated mean assimilation efficiencies for the six non-predatory species ranged from 18 to 74% although considerable variation between replicate analyses (standard errors between 6.4 and 19.3% of the mean) was obtained for all species. The possibility that decreases in ^{14}C activity relative to ^{144}Ce measured in faecal collections could be accounted for solely by metabolism of gut microflora rather than absorption by the animal itself was checked in a further experiment with *Deleatidium* larvae. Following 24 and 48 h feeding periods, guts were dissected from larvae and body

Table 3.1 Ingestion rates and assimilation efficiencies of eight aquatic invertebrate species fed on stone surface organic layers formed in the dark and labelled with ^{144}Ce and ^{14}C-glucose. Experiments were carried out at 10°C ± 2°C for 24 h.

Species	Replicate experiments	Feeding mode	Ingestion rate ($\mu g.mg^{-1}$ larvae.hr^{-1} ± 1SE)	Assimilation Efficiency (% ± 1SE)
Plecoptera				
Stenoperla prasina	5	Predator	-	-
Spaniocerca zelandica	5	Browser	6.8 ± 0.6	69 ± 9
Ephemeroptera				
Deleatidium sp.	11	Browser	5.0 ± 0.9	62 ± 4
Trichoptera				
Pycnocentrodes aureola	3	Browser	3.8 ± 0.6	18 ± 2
Philorheithus agilis	3	Predator	-	-
Coleoptera				
Helodid Species A	5	Browser	2.5 ± 0.3	30 ± 3
Helodid Species B	4	Browser	2.8 ± 0.4	31 ± 6
Mollusca				
Potamopyrgus antipodarum	8	Scraper	3.1 ± 1.0	74 ± 11

radioactivity compared with that of non-feeding controls. On average, body counts were 9× higher in feeding larvae indicating substantial absorption of ^{14}C through the gut wall.

Larvae of *Deleatidium* were also used in another experiment in which the heterotrophic (^{14}C-bicarbonate labelled) components of stone surface organic layers in which the nature and density of the algal community differed (Table 3.2) were labelled and fed on by larvae.

Ingestion rates were comparable in most cases to those recorded from animals fed on layers formed in the dark at Middle Bush Stream, and were lowest where high density, filamentous green algae were present. *Deleatidium* larvae appear to feed primarily by sweeping material into their mouths with heavily fringed maxillae and attached algal filaments are not easily ingested in this manner.

Mean assimilation efficiencies calculated for larvae fed ^{14}C-glucose labelled layers of the three types ranged from 47-58% but considerable variability between replicates was found and means were not significantly different ($P < 0.05$) (Table 3.2).

Assimilation efficiencies for ^{14}C-bicarbonate labelled stones differed substantially between treatments. Filamentous algae were poorly assimilated whereas diatoms (mainly *Rhoicosphenia* and *Cocconeis*) were present on "low density" stones and high efficiencies were recorded. Medium density stones were colonised by diatoms and filamentous algae and animals fed on them had intermediate assimilation efficiencies.

When both ^{14}C-glucose and ^{14}C-bicarbonate were used simultaneously, mean assimilation efficiencies between 30 and 48% were obtained (Table 3.2).

DISCUSSION

The organic layers which formed on stone surfaces in field and laboratory channels consisted of slime, fungi, bacteria, algae and fine particulate matter interwoven together and thus conforming to the general descriptive model of Madsen (1972). Comparable, but apparently thicker layers have been described by Karlström (1978) from a fifth order Danish forest stream while Pennak (1977) observed layers of "lithophyton" varying in thickness in a variety of Rocky Mountain streams. Thin surface films incorporating abundant slime and associated bacterial and algal cells have been described from steep subalpine streams in Canada by Geesey *et al.* (1978).

Table 3.2 Ingestion rates and assimilation efficiencies of *Deleatidium* sp. (mayfly) fed on stone surface organic layers with varying algal communities and densities labelled with ^{144}Ce and ^{14}C-glucose and/or ^{14}C-bicarbonate.

	^{14}C-glucose		^{14}C-bicarbonate		^{14}C-glucose and ^{14}C-bicarbonate	
	Assimilation efficiency (% ± 1SE)	Ingestion rate ($\mu g.mg^{-1}$ larvae.hr^{-1}) ± 1SE	Assimilation efficiency (% ± 1SE)	Ingestion rate ($\mu g.mg^{-1}$ larvae.hr^{-1}) ± 1SE	Assimilation efficiency (% ± 1SE)	Ingestion rate ($\mu g.mg^{-1}$ larvae.hr^{-1}) ± 1SE
Low density (5.06 mg.m^2 chl *a*)	58 ± 9	4.7 ± 0.6	68 ± 24	4.3 ± 1.1	48 ± 17	4.9 ± 0.6
Medium density (30.8 mg.m^2 chl *a*)	53 ± 12	5.3 ± 1.3	21 ± 4	5.1 ± 1.3	40 ± 8	4.3 ± 0.8
High density (64.8 mg.m^2 chl *a*)	47 ± 11	1.8 ± 0.4	6 ± 3	1.6 ± 0.3	30 ± 11	1.1 ± 0.3

Under conditions of high light intensity, filamentous algae and diatoms were visually the dominant components of the layer but in the darker forest stream channel diatoms were the only autotrophs present. Even in total darkness an organic layer will develop and in Middle Bush Stream this was predominantly a coating of slime up to 80 µm thick in which was trapped and embedded fine detrital fragments, diatom frustrules, fungal hyphae and less visible (but possibly abundant) bacteria.

Layers grown in the dark by Karlström (1978) also were dominated by a "mucoid layer" and contrasted with the more complex, multi-layered structures which developed under natural lighting regimes. Although the attention of stream ecologists concerned with the feeding of grazing benthic invertebrates traditionally has focused on the autotrophic components of the periphyton (e.g., Hynes, 1970; Hawkins & Sedell, 1981), heterotrophically based layers also are likely to play a significant role in this respect. The lower surfaces of stones and coarse sub-surface sediments can be expected to support surface films of this kind and they are likely to be grazed by invertebrates whose presence, often at considerable depths within the bed, is now well established (Williams & Hynes, 1974). In New Zealand, benthic stream faunas are dominated by species which colonise hard substrates and feed primarily by browsing over their surfaces (Winterbourn *et al.*, 1981, Chapter VI). Where algal populations are maintained they can provide an important source of ingested and metabolised food (Chapter IV) but, in many small forest streams where little light reaches the stream bed, heterotrophically-based organic layers must represent major sources of food. Similarly, in highly unstable streams, regardless of the degree of shading, algae may be a limited resource (Cowie, 1980; Rounick & Gregory, 1981) whereas heterotrophic layers appear to persist (Cowie, 1980) and are more likely to assume a major role in energy transfer to consumers.

The field experiments carried out under varying light regimes, and in waters of differing DOC and POC content, resulted in the formation of organic layers varying in thickness and biomass, and in the relative proportions of biotic-abiotic and autotrophic-heterotrophic components. The importance of DOC derived from algae as a carbon source was suggested by results obtained at the spring site where levels of DOC in spring water were very low. Thus, in the dark channel where algae could not grow, few bacteria or fungi were found whereas in the light channel, bacteria were abundant particularly at intercellular junctions on algal filaments. Several workers have contended that secretions from aquatic autotrophs

(macrophytes - Allen [1971], Allanson [1973]; algae - Geesey *et al.* [1978]) were significant sources of DOM utilised by bacteria and fungi in associated aufwuchs communities, and a complementary role is indicated by my results. Further, the central role of DOC in layer formation was demonstrated.

In Middle Bush, "slime" rapidly colonised stone surfaces in both light and dark channels but its origin and nature are not well understood. The work of Geesey *et al.* (1978) and Barton & Lock (1979) indicates that slime is predominantly a polysaccharide produced by colonising bacteria and/or algae, and chemical analyses of slime dominated Middle Bush Stream layers grown in the dark for one month showed them to be 75% carbohydrate by weight. My observations, particularly those made in laboratory channels, indicated a close spatial and temporal relationship between slime and bacterial rods while increases in slime production also were correlated with a decline in water column DOC. This suggested that DOC was being utilised by bacteria as an energy source, thereby stimulating their growth and metabolism and resulting in increased slime production.

DOC may also be incorporated into organic layers by precipitation, complexing and flocculation processes (Lush & Hynes, 1973; Paul *et al.*, 1977; McCammon, 1978) or, as demonstrated by Khailov & Finenko (1970), it may be adsorbed onto stone surfaces abiotically as shown in the formalin treated laboratory channels.

The relative significance of biotic and abiotic uptake mechanisms has been a matter of some debate (Dahm, 1981) but, in my experiments, uptake was predominantly biotic as was layer formation which did not occur in the sterile (formalin-treated) channel. This is in general agreement with Dahm's (1981) finding that adsortive abiotic mechanisms were kinetically faster than biotic uptake although he found that over a longer period of time (48 h) microbial uptake predominated.

Of particular interest is my finding that a number of the common stream invertebrates tested were able to feed effectively on very thin organic layers incorporating little or no algae. It is well known that many stream insects feed on periphytic algae (e.g., Brown, 1960; Cummins & Klug, 1979; Anderson & Cummins, 1979) but only the work of Madsen (1974) and Iversen & Madsen (1977) with two species of Plecoptera has demonstrated the nutritional value of predominantly heterotrophic organic layers to stone surface dwelling macroinvertebrates. The calculated ingestion rates of 5.0 and 3.1 $\mu g.mg^{-1}$dw larvae.hr^{-1} for *Deleatidium* and *Potamopyrgus antipodarum* fed on thin, predominantly heterotrophic layers fall within the range (1.3 - 6.4 $\mu g.mg^{-1}$ dw larvae.hr^{-1}) reported for larvae of the mayfly *Stenonema*

pulchellum and two freshwater limpets, *Ancylus fluviatilis* and *Laevapex fuscus* grazing periphyton (Trama, 1972; Calow & Fletcher, 1972; McMahon, 1975).

Caution must be exercised in accepting the exact assimilation values calculated from data obtained in the dual-tracer experiments since the uneven distribution of materials within the organic layer made homogeneous labelling with ^{14}C, as opposed to ^{144}Ce, impossible (Sedell, 1971). Nevertheless, effective utilisation of labelled material is indicated by the calculated mean assimilation efficiencies of 62% for *Deleatidium* and 74% for *Potamopyrgus* fed "heterotrophic" organic layers. These efficiencies are lower than the 88% calculated for *A. fluviatilis* fed periphyton (Calow & Fletcher, 1972) but exceed those reported for *S. pulchellum* fed periphyton (53%; Trama, 1972), *Tricorithodes minutus* (Ephemeroptera) fed diatoms and blue-green algae (33-57%; McCullough *et al.*, 1979) and the oligochaete, *Dendrobaena rubida* fed on bacterial and fungal film from a percolating filter (35%; Solbé, 1971).

As has been pointed out elsewhere (Winterbourn *et al.*, 1981), insects which feed directly on coarse leaf detritus are poorly represented in New Zealand streams, and one consequence of this is that fine particulate organic matter produced as a result of shredder feeding activity (Short & Maslin, 1977) is rarely available to smaller detritivores as a source of food. Many New Zealand benthic invertebrates occur predominantly on stony substrata, and the organic layers on stone surfaces appear to be their principal feeding sites. This clearly is the case for most larval Leptophlebiidae (Ephemeroptera) including *Deleatidium*, Gripopterygidae (Plecoptera) and Chironomidae which frequently predominate numerically in streams and attests to the importance of organic layers in overall stream productivity.

Research in the next chapter was conducted in an effort to understand the sources of carbon utilised by invertebrates in contrasting streams. Minshall (1978), in a contentious paper, suggested that the importance of autochthonous inputs to small streams has been underestimated for various reasons. With this in mind, stable carbon isotope analysis was used to examine utilisation of both allochthonous and autochthonous carbon by invertebrates where the magnitude of these inputs vary.

CHAPTER IV

DIFFERENTIAL UTILISATION OF ALLOCHTHONOUS AND AUTOCHTHONOUS INPUTS BY AQUATIC INVERTEBRATES IN SOME NEW ZEALAND STREAMS: A STABLE CARBON ISOTOPE STUDY

INTRODUCTION

Trophic relationships of benthic stream invertebrates have been the subject of many studies. Early workers such as Percival & Whitehead (1929), Badcock (1949) and Jones (1950) observed that algae and detritus of both allochthonous and autochthonous origin comprised much of the material ingested by a wide range of species. Several recent studies have stressed the importance of allochthonous inputs as the primary sources of carbon utilised as food in woodland streams (e.g., Minshall, 1967; Cummins, 1974). However, significant autotrophic production can occur in many streams and rivers (Minshall, 1978) and since algal populations turn over rapidly, much dead algal material must enter the detrital pool. In desert streams, detritus of autochthonous origin predominates (Busch & Fisher, 1981) whereas in heavily shaded forest streams most detrital material is terrestrial in origin (Fisher & Likens, 1973). Most stream environments probably fall between these two extremes and both kinds of detritus undoubtedly occur. The questions arise, can or do particular species utilise both allochthonously and autochthonously derived detritus as food, and if not, are some species restricted to certain kinds of stream for this reason?

The main aim of my study was to investigate the energy utilisation of benthic invertebrates in contrasting streams where the relative contributions of allochthonous and autochthonous inputs were markedly different. I approached this problem using stable carbon isotope analysis which has been used successfully for elucidating marine, estuarine and terrestrial food chain relationships (Haines, 1976; McConnaughey & McRoy, 1979; Tieszen *et al.*, 1979), and for identifying carbon sources in terrestrial (Boutton *et al.*, 1980) and aquatic ecosystems (Rau, 1980). In terrestrial ecosystems this is because plants using C_3 and C_4 photosynthesis pathways exhibit distinct carbon isotope ratios (-21 to -33 per mille vs PDB, and -9 to -17 per mille vs PDB, respectively) (Boutton *et al.*, 1980). Since the $^{13}C/^{12}C$ ratios of terrestrial plants are also distinct from those of aquatic algae (Rau, 1980), as a result of the ^{13}C-depleted HCO_3^- source utilised by aquatic plants, this provides a basis for identification of food utilisation of aquatic animals. This is because only a small increase in $^{13}C/^{12}C$ has been found in animals relative to their food (DeNiro & Epstein, 1978). A further advantage of stable carbon isotope methodology is that animal tissues provide a summary of their previous feeding history, not simply what they ingest (as observed for an instant in time by gut analysis) but what materials are utilised for tissue growth.

A subsidiary aim of this work was to investigate whether large-scale watershed practices (clear-cutting and burning) resulting in increased authochthonous primary production were reflected by the $^{13}C/^{12}C$ ratios of the invertebrate fauna.

STUDY SITES

Animals and potential foods for stable carbon analysis were obtained from nine streams in the South Island of New Zealand. The principal sites at which the most extensive collections were made were Middle Bush Stream and Grasmere Stream, located about 1 km apart in the Cass basin, western Canterbury (43°02'S, 171°46'E). Middle Bush Stream drains a 28 ha catchment of subalpine scrub, tussock and bare scree slope and includes a 3-4 ha stand of mountain beech (*Nothofagus solandri* var. *cliffortioides* (Hook.f.) Poole) through which the stream flows. In the forest the stream is well shaded (Table 4.1) with a rough boulder-strewn bed and steep banks (Figure 4.1a). Large amounts of coarse particulate allochthonous material, particularly beech leaves and twigs, enter the stream throughout the year (Winterbourn, 1976; McCammon, 1978) and autochthonous primary production is low (Cowie, 1980; unpublished data). The stream fauna is dominated by larval insects with species of Ephemeroptera, Plecoptera, Trichoptera and Diptera-Chironomidae being most common (see Davis & Winterbourn, 1977; Winterbourn, 1978b).

Grasmere Stream is larger than Middle Bush Stream (Figure 4.1b, Table 4.1) and for much of its length flows through tussock-grassland. Its sources are two small lakes (Sarah and Grasmere) and several beds of *Phormium tenax* and *Typha orientalis* occur along the upper course. In its middle reaches where collections were made the bed is predominantly gravel and larger stones. The stream supports a high standing crop of benthic algae throughout the year and localised beds of macrophytes including *Elodea canadensis*, *Ranunculus fluitans*, *Potamogeton cheesmanii* and *Myriophyllum propinquum*. The invertebrate fauna is dominated by species of Trichoptera, Ephemeroptera, Chironomidae and a gastropod, *Potamopyrgus antipodarum*.

All additional study sites were located west of the main alpine divide near the towns of Reefton and Ahaura. Callaghans Creek in the Hochstetter State Forest (42°24'S, 171°33'E) is a low-gradient stream similar in size to Middle Bush Stream with a stable, stony bed. Collections were made at two sites - (a) in the lower reaches where it flows through dense beech forest and is heavily shaded, and (b) in the

Figure 4.1a A section of Middle Bush Stream in mountain beech forest.

Figure 4.1b Grasmere Stream flowing through tussock-grassland.

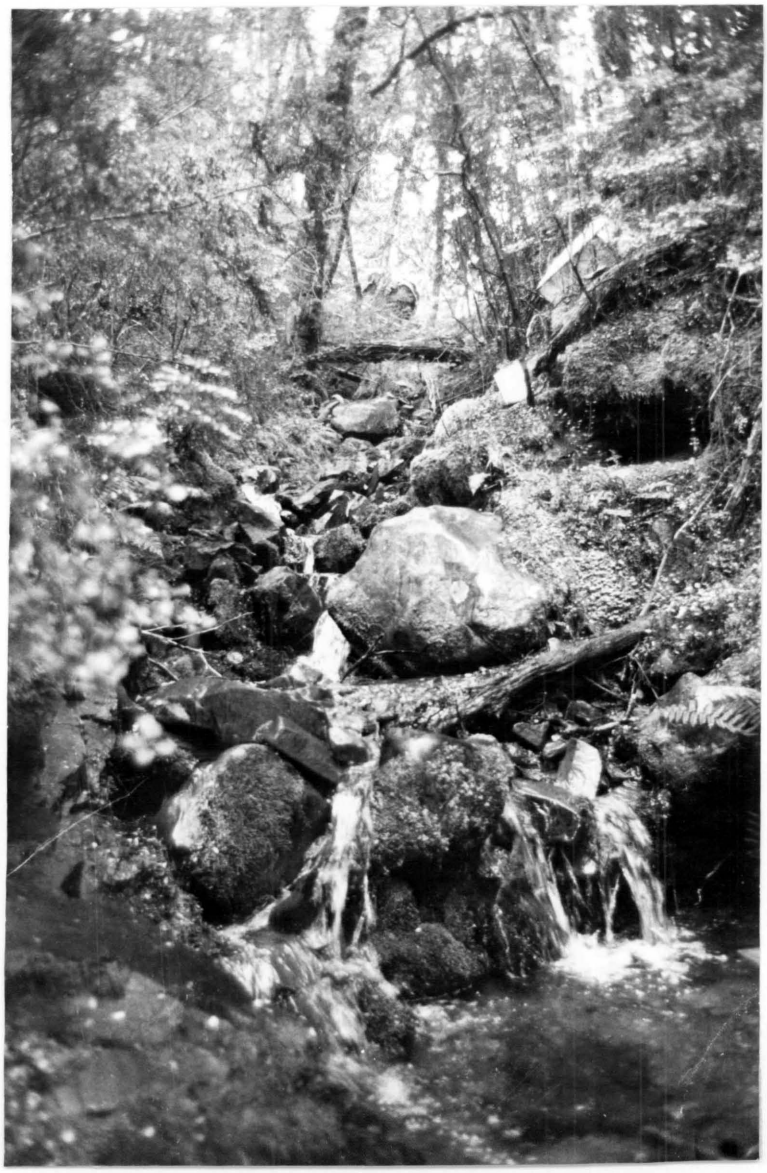


Table 4.1 Environmental data measured for Middle Bush and Grasmere Streams.

	Middle Bush Stream	Grasmere Stream
Discharge[a] ($\ell.sec^{-1}$)	4	124
Mean width (m)	1	2.8
Mean depth (m)	0.25	0.40
Alkalinity ($\mu g.ml^{-1}$ $CaCo_3$)	37.2	34.6
pH	6.8	6.4
Annual temperature range (°C)	1-14	5-17
% Shading	80	5
Light input[b] (langleys.day^{-1})	14	58
Dominant algal genera	*Rhoicosphenia, Cocconeis*	*Cladophora, Melosira, Gomphonema*
Algal standing crop[c] ($g.m^{-2}$)	0.38 ± SE 0.11	2.94 ± SE 0.43
Primary course particulate input	Beech	Tussock

a Mean summer discharge

b Estimated for 24 hr autumn day using method in Rounick & Gregory (1981)

c Maximum autumn standing crop levels

headwaters where the original vegetation has been replaced 10 years ago by exotic Monterey pines (*Pinus radiata*).

All other collections were made in small, primary tributaries within the New Zealand Forest Service's Maimai Experimental Catchment Area (see Neary *et al.*, 1978). The streams drain catchments ranging from 1.6 to 8.3 ha, all of which supported beech-podocarp-hardwood forest prior to 1976. Subsequently, a number have been logged and in some cases burnt and replanted with *P. radiata* and eucalypts (*Eucalyptus delegatensis*). Collections were made from two control and four logged catchments (see Table 4.3 for details). All streams had predominantly gravel substrates and very low discharge at the time of sampling (1-4 $\ell \cdot s^{-1}$), but varied in degree of shading, development of benthic algal populations and inputs of forest litter.

METHODS

Invertebrates and potential foods for isotope analysis were collected from Middle Bush and Grasmere Streams at intervals over a period of eight months (October 1980 - June 1981). For some insect species, late instar larvae were taken but whenever possible adults and pupae were obtained, as they should provide a summary of an insect's trophic history in their tissues. Both potential foods and animals were preserved soon after collection by freezing; molluscs after they had egested their gut contents. Single collections were made from Callaghans Creek and the Maimai Experimental Catchments in May 1981. They consisted of pupae and late instar larvae as well as potential foods.

Riparian vegetation sampled included pine needles (*P. radiata*), leaves of tussock (*Festuca novae-zelandiae*), beech leaves and beech wood which had been submerged in Middle Bush Stream for three years. Beech leaves were collected from living trees, the forest floor and in water on the stream bed. Samples of three aquatic macrophytes were taken from Grasmere Stream. Fine particulate organic matter (FPOM; 0.45 µm - 1.0 mm) was collected at Middle Bush Stream and Grasmere Stream in stone-filled containers which were sunk into the stream beds for a month. At the other sites, FPOM was obtained in sediment cores and passed through a 1 mm mesh sieve. Algae and associated materials were scraped from stones and from glass slides which had been left in the Cass streams for a month. An almost pure algal sample was obtained by thoroughly washing a clump of *Cladophora* from Grasmere Stream.

Leachate for isotope analysis was obtained by soaking pre-abscission beech leaves in *ca.* 10 ℓ of non-sterile distilled water for 24 h. The concentrated leachate was filtered (0.45 μm) to remove any FPOM and freeze-dried. Finally, one litre samples of Middle Bush and Grasmere Stream water were collected for dissolved inorganic carbon (DIC) isotope analysis. Water samples were filtered in the field (0.45 μm) and stored in the dark in full, airtight, glass bottles at <4°C for up to seven days. DIC was precipitated as $SrCO_3$ from which CO_2 was evolved with acid for mass spectrometric analysis.

In preparation for analysis, materials were unfrozen, and guts dissected from insect larvae to remove undigested food. Any materials suspected of containing carbonates were acidified with 1N HCl. Up to 50 individuals of each species from each site were pooled, freeze-dried, pulverised and stored in a desiccator. At the Institute of Nuclear Sciences laboratory, 3-5 mg subsamples were oxidised in sealed quartz "vycor" tubing using a break-seal method (Buchanan & Corcoran, 1959). The resulting CO_2 was purified and analysed in a Nuclide 6-60 ratio mass spectrometer. Results are reported as the relative per mille difference between the isotope ratio of the sample and that of the international PDB standard (Craig, 1957), expressed as follows:

$$\delta^{13}C_{PDB} = \left(\frac{(^{13}C/^{12}C)_{sample}}{(^{13}C/^{12}C)_{PDB}} - 1 \right) \times 1000 \text{ per mille}$$

The more negative the $\delta^{13}C$ value the greater the ^{13}C depletion. Analytical precision was judged on the basis of eleven replicates of a graphite standard (NBS-21) analysed over a period of three months ($\bar{X}$ = -27.99 per mille, 1 S.D. = 0.12, range = 0.36). Replicates of potential food and animals placed randomly in the processing order never differed by ±0.4 per mille.

RESULTS

Middle Bush Stream

δ^{13} values obtained for invertebrates and allochthonous food materials collected from Middle Bush Stream ranged from -29.5 to -23.9 per mille and -27.5 to -25.0 per mille respectively (Table 4.2). Laboratory produced mountain beech leachate was slightly more ^{13}C-enriched (-25.3 per mille) than the other carbon sources. Beech leaves at

different stages of decomposition showed progressive ^{13}C enrichment, ranging from -30.7 per mille for living leaves to -27.3 per mille for those submerged and decomposing in the stream. Beech wood which had been in the stream for three years was even more ^{13}C enriched at -25.0 per mille.

The $^{13}C/^{12}C$ ratios of invertebrates from Middle Bush Stream reflected the ratios of allochthonous materials (Table 4.2). *Limonia nigrescens*, a tipulid which inhabits decaying beech logs was most ^{13}C enriched (-23.9 per mille), and its $^{13}C/^{12}C$ ratio closely corresponded to that of the wood. Least ^{13}C enrichment was observed in *Deleatidium* sp., a browsing mayfly which was abundant on stones in riffles. The two large, leaf and bark shredding caddisflies, *Oeconesus maori* and *Zelandopsyche ingens* had $\delta^{13}C$ values close to those of their suspected foods, as did the leaf-shredding stonefly, *Austroperla cyrene*. All predatory insect larvae possessed ratios close to those of their probable prey.

Stable carbon isotope data from Callaghans Creek (Table 4.2) also indicated a close relationship between allochthonous organic materials and invertebrates in both the beech and pine vegetated sections of the catchment.

Grasmere Stream

$\delta^{13}C$ values for potential foods from Grasmere Stream ranged from -35.0 to -23.6 per mille, all materials being depleted in ^{13}C relative to Middle Bush samples with the exception of tussock. Greatest ^{13}C depletion (-35.0 per mille) was found in a sample of filamentous algae from which entrapped fine particles had been washed.

Grasmere Stream invertebrates had $\delta^{13}C$ values ranging from -35.8 to -29.2 per mille suggesting variable dependence on autochthonous and allochthonous materials as food. *Pycnocentria evecta*, a caddisfly whose browsing larvae ingest large amounts of algae showed the greatest ^{13}C depletion whereas deposit feeding Chironomidae and Oligochaeta were most ^{13}C enriched. $\delta^{13}C$ values for predatory insects were variable (-32.4 to -29.3 per mille), and an average 5-6 per mille lighter than those for insect predators from Middle Bush Stream. Overall, it is clear that related species from Grasmere Stream showed a higher dependence on autochthonously derived foods (algae, macrophytes) than did those from Middle Bush.

Table 4.2 δ^{13} values of potential foods and invertebrates from four sites. Invertebrate feeding mode is represented as follows: CB - collector-browser; O - omnivore; P - predator; S - shredder.

	Feeding mode	Middle Bush Stream	Grasmere Stream	Callaghans Creek (Beech forest)	Callaghans Creek (Pine plantation)
Potential Foods					
Beech leaves (living tree)		-30.7			
Beech leaves (forest floor)		-28.5			
Beech leaves (stream conditioned)		-27.3			
Beech wood conditioned for 3 years		-25.0			
Beech leachate		-25.3			
Pinus radiata needles					-29.1
FPOM (<1 mm >0.45 µm)		-27.2	-29.1	-28.8	-28.4
Dissolved inorganic carbon		-11.1	-12.1		
Stone organic layer		-26.0	-33.2		
Fissidens rigidulus (C. Müeller)		-29.8			
Cladophora sp.			-35.0		
Myriophyllum propinquum A. Cunn.			-26.8		
Elodea canadensis Michx.			-31.1		
Festuca novae-zelandiae Cock.			-23.6		
Invertebrates					
Oligochaeta					
Eiseniella tetraedra (Savigny)	CB	-24.7	-29.3		
Gastropoda					
Potamopyrgus antipodarum (Gray)	CB		-34.5		
Decapoda					
Paranephrops planifrons White	O			-26.2	

Cont'd/...

Ephemeroptera					
Coloburiscus humeralis (Walker)	CB		-33.6	-26.1	-27.4
Deleatidium sp.	CB	-29.5	-35.2	-29.2	-29.0
Plecoptera					
Austroperla cyrene (Newman)	S	-26.2			
Spaniocerca zelandica Tillyard	CB	-24.9			
Stenoperla prasina (Newman)	P	-25.9			
Zelandobius confusus (Hare)	CB		-31.1		
Z. furcillatus Tillyard	CB	-23.9			
Megaloptera					
Archichauliodes diversus (Walker)	P			-26.8	-28.4
Trichoptera					
Aoteapsyche colonica (McLachlan)	CB		-33.2		
Edpercivalia maxima (McFarlane)	P	-25.2			
Hudsonema amabilis (McLachlan)	O		-30.7		
Hydrobiosis clavigera McFarlane	P		-32.4		
Hydrobiosella stenocerca Tillyard	CB	-25.5			
Hydrobiosis sp.	P	-25.7	-31.1		
Neurochorema confusum (McLachlan)	P		-29.4		
Oeconesus maori McLachlan	S	-26.1			-28.1
Olinga feredayi (McLachlan)	CB	-25.6	-31.5		
Philorheithrus agilis (Hudson)	P	-24.7			
Polyplectropus puerilis (McLachlan)	O		-30.0		
Psilochorema sp.	P		-29.3		
Pycnocentria evecta McLachlan	CB		-35.8		
Triplectides obsoleta (McLachlan)	S			-28.5	-29.6
Zelandopsyche ingens Tillyard	S	-27.1		-25.6	
Diptera					
Chironomidae	CB		-29.2		
Limonia nigrescens (Hutton)	S	-23.9			
Coleoptera					
Helodidae Species A	CB	-25.9			

Table 4.3 δ^{13} values of potential foods and invertebrates from six catchments in the Maimai Experimental Catchment Area. Feeding modes as in Table 4.2.

Catchment number Treatment(s)	Feeding mode	205 Logged 1978 Planted 1978	206 Control	207 Logged 1976 Burnt 1977 Planted 1977	208 Logged 1979 Burnt 1980 Planted 1980	214 Logged 1977 Burnt 1978 Planted 1978	215 Control
Potential Foods							
Algae						-32.5	
FPOM		-27.9	-27.2	-28.1	-27.4		-28.1
Invertebrates							
Plecoptera							
Austroperla cyrene	S	-31.8			-25.4		
Stenoperla prasina	P	-29.4		-28.5	-27.0		-27.3
Trichoptera							
Hydrobiosella stenocerca	CB				-25.8		
Oeconesus maori	S				-24.9		
Hydrobiosis sp.	P					-28.5	
Triplectides obsoleta	S	-29.4					
Zelandopsyche sp.	S						-27.8
Ephemeroptera							
Deleatidium sp.	CB	-32.9	-29.3		-30.4	-35.3	-28.5
Megaloptera							
Archichauliodes diversus	P			-27.1			
Decapoda							
Paranephrops planifrons	O	-23.9	-28.6				-25.8

Maimai Experimental Catchments

$\delta^{13}C$ values for common aquatic invertebrate species and their potential foods from tributaries in the Maimai experimental area are shown in Table 4.3. The streams drain catchments which vary in management treatment (burnt or not burnt), age of cut, and time of replanting, factors which could be expected to affect the availability of different foods.

The mayfly *Deleatidium* was most ^{13}C depleted in the earliest logged catchment, and the $\delta^{13}C$ value of -35.3 per mille indicates that algae were a major source of carbon utilised there. On the other hand, *Deleatidium* from streams in unlogged and more recently logged catchments, where considerable allochthonous debris was still present in the channels, had higher $\delta^{13}C$ values. These were similar to those found in *Deleatidium* from Middle Bush Stream and Callaghans Creek, and indicated greater allochthonous food dependence. It is of particular interest to note that the same trend was shown also by *Stenoperla prasina*, the major invertebrate predator in these streams. This stonefly probably feeds to a large extent on *Deleatidium* as in other streams (Winterbourn, 1974; Devonport & Winterbourn, 1976). Shredders were not found in streams draining the earlier-logged catchments where little coarse organic debris remained. $\delta^{13}C$ values of insects taken from the control and 1979-logged catchments indicated a continued dependence on allochthonous materials whereas some utilisation of more ^{13}C-depleted carbon sources by *Triplectides obsoleta* and *Austroperla cyrene* was apparent in the 1978-logged catchment 205.

DISCUSSION

The success of this study depended on the existence of a measurable isotopic distinction between allochthonous and autochthonous carbon sources at the study sites. $\delta^{13}C$ values of potential, allochthonous foods were all about -27 per mille as expected for terrestrial C_3 plants (Boutton *et al.*, 1980).

In contrast, $\delta^{13}C$ values for algae and aquatic macrophytes approached -35 per mille, a result of the ^{13}C-depleted HCO_3^- source utilised by aquatic plants. Biogenic (respiration) CO_2, depleted in ^{13}C can also contribute to the inorganic carbon pool utilised by aquatic producers and so lower $\delta^{13}C$ values further (Rau, 1978). However, since $\delta^{13}C$ values for dissolved inorganic carbon in water samples from Middle Bush and Grasmere Streams

(-11.0 and -12.1 per mille, respectively) were within the range expected for river water with isotope exchange with atmospheric carbon dioxide (Mook, 1970), it is apparent that biogenic CO_2 was not a significant source of ^{13}C depletion in this study.

The $\delta^{13}C$ data obtained demonstrated quite clearly the linkages between primary carbon sources and consumers at the study sites. Since they give a summary of an animal's trophic history, they also offer insights not provided by more traditionally employed methods. While radiotracers can provide information on utilisation of selected materials under controlled conditions, they have only limited application in the field. Gut content analyses provide an instantaneous picture of food recently ingested, but tell nothing about the utilisation of that food. Stable carbon isotope analysis can overcome some of those limitations although, at least in the way I have been using it, the technique is restricted to evaluation of food relationships at a relatively coarse (i.e., autochthonous vs allochthonous) level. This is because $\delta^{13}C$ values of potential foods compared must be distinct.

The $\delta^{13}C$ values for Middle Bush invertebrates indicated a clear dependence on terrestrial vegetation as food. This was not unexpected as allochthonous materials are generally regarded as being the principal sources of carbon supporting the benthic communities of small, forested streams (e.g., Cummins, 1974). However, the relatively ^{13}C-depleted values obtained for *Deleatidium* at all forested sites suggests that this species is less dependent on terrestrial carbon than the other species examined. *Deleatidium* larvae feed on stone surface organic layers which consist of bacteria, fungi, fine particulate detritus, polysaccharide slimes and diatoms. The heterotrophic and allochthonously derived components of the layer would have a $\delta^{13}C$ value of about -26 per mille whereas the value for diatoms is expected to be about -33 per mille. The larvae appear to ingest materials non-selectively as indicated by gut content analysis (Cowie, 1980; unpublished data). However, the ^{13}C-depleted values obtained for *Deleatidium* tissue (-29 to -35 per mille) indicate that diatoms are assimilated selectively or more efficiently, a condition which is not apparent from an examination of gut contents alone. This is in accordance with Greig's finding (1976) that *Deleatidium* larvae assimilate diatoms with a high efficiency, *ca.* 65%. This illustrates one of the strengths of the stable carbon isotope methodology, and is analogous to the findings of Rau & Anderson (1981) that leachate represented an important source of "invisible" carbon incorporated into a laboratory

population of the caddisfly *Clistoronia magnifica* (Banks). On the other hand, it should be remembered that the only carbon available for analysis is that which is incorporated into the insect's body tissue. Although, animals do not fractionate the carbon isotope composition of their food (DeNiro & Epstein, 1978) it is possible that different foods are utilised in different ways (e.g., incorporation into body tissue or immediate oxidation). Stable carbon ratios will only reflect those sources of food incorporated into body tissue.

In Middle Bush Stream, *Deleatidium* larvae can constitute over 50% of the animals taken in benthic samples and up to 10% of the invertebrate biomass (unpublished data). This indicates that despite its low standing biomass (<0.3 g m^{-2}, Table 4.1) algal production can support substantial secondary production. This is possible since turnover of algal populations is rapid in comparison with rates of insect growth (McIntire, 1973), and provides further evidence to support Minshall's (1978) view that the role of autotrophs as a source of energy to consumers should not be underestimated in apparently "heterotrophic" streams.

The sources of organic carbon utilised by primarily detritus-feeding invertebrates in Grasmere Stream are more difficult to determine since detritus includes material of algal, aquatic macrophyte and terrestrial origin present in various proportions. The $\delta^{13}C$ value of -29.1 per mille for the sample of FPOM analysed indicated that it included material of allochthonous and autochthonous origin. Using Rau's (1980) proportional method it can be calculated that the former made up 53-76% depending on the ratio of algal to macrophyte-derived material present. In addition, the composition of FPOM is likely to vary spatially and seasonally, reflecting climatic and phenological phenomena.

Grasmere Stream invertebrates were all depleted in ^{13}C compared with those from forested sites, and the range of $\delta^{13}C$ values recorded indicate variable dependence on allochthonous and autochthonous materials. This was supported by gut analyses. The gastropod, *Potamopyrgus antipodarum* showed a high level of dependence on algae as a source of carbon ($\delta^{13}C$ = -34.5), and Wisely (1961) suggested that its faeces may represent a major source of food for the filter-feeding mayfly, *Coloburiscus humeralis* in this stream. The plausibility of this suggestion is supported by the stable carbon data (Table 4.2).

Results obtained from the Maimai experimental catchments show the value of stable carbon isotope analysis for investigating trophic responses of stream invertebrate communities to environmental change. My results,

which are of only a preliminary nature, provide an indication of the time scale involved in adjustment by the fauna to a change in energy base. Thus, age of cut was important in determining the type of material utilised. The most ^{13}C-depleted insects occurred in the earliest logged catchment (five years prior to sampling), reflecting the increased role of algae in their diets. This in turn is a consequence of greater benthic primary production reduction in forest inputs and the efficient flushing of forest-derived organic materials from the stream by sequential floods. In contrast, stable carbon ratios of invertebrates from the most recently logged catchment (two years before sampling) were similar to those of animals from control catchments and indicated little shift in food dependence in this short time.

It is also of interest to note that changes in the nature of the food base following catchment vegetation removal apparently had little impact on the species composition of the Maimai stream communities. Thus, with the exception of the oeconesid caddisflies which are obligate large particle detritivores, whose source of food was removed by logging (and, in the case of stored materials, floods), no losses or gains of species or marked changes in relative abundance were apparent (unpublished surveys). This is in contrast to several recent North American studies (e.g., Webster & Patten, 1979; Newbold *et al.*, 1980) and in part may be a consequence of the relatively short time which had elapsed since logging. Nevertheless, it is consistent with observations on the nature of New Zealand stream faunas in general (Winterbourn *et al.*, 1981 [Chapter VI]) which indicate that a nucleus of common genera and species prevail in many streams whether they be in indigenous beech, kauri, or podocarp-hardwood forests, pine plantations or predominantly grassland. Many of these species clearly possess considerable ecological flexibility with respect to habitat requirements, life history patterns and, as indicated by gut analyses and the present work, food requirements. Although plant material of various origins is ingested by many species and converted to animal tissue, it will vary in quality and hence is likely to affect growth as demonstrated by Ward & Cummins (1979) and Fuller & Mackay (1981). If so, differences in growth rates and life history patterns of a species might be expected at different sites reflecting in part the nature and quality of the available carbon sources. Such an explanation could help explain the different life history patterns of stoneflies recorded by Cowie (1980) at forested and open sites within a single New Zealand river system.

In future, refinements and improvements in the application of stable carbon isotope methodology to ecosystem studies are likely to be forthcoming. Analysis of insect larvae at different stages of development, and at different times of year should enable changes in food dependence within the life history of a species to be assessed. Further, it is conceivable that analysis of predators alone could provide a useful "short-cut" method for determining the sources of carbon supporting benthic communities since the $\delta^{13}C$ values of predators reflect the trophic linkages beneath them. In combination with quantitative field estimates of animal numbers and biomass, $\delta^{13}C$ data also provides a means by which the energy basis for secondary production can be determined. Because the carbon isotope method discriminates between carbon sources at a relatively coarse level (e.g., allochthonous vs autochthonous), it has limited application in studies of specific food chain linkages. However, because the insights into trophic dependence it provides are broad, and applicable at a community or ecosystem level of investigation, stable carbon analysis would appear to have great potential as a management tool.

One goal of this thesis was to use the understanding acquired in the course of my research to suggest management plans, backed by supporting scientific evidence, for use by parties involved in logging - stream conservation decisions. An examination of the linkage between forest vegetation, stream geomorphology and invertebrates therefore was undertaken and is presented in this section.

CHAPTER V

BENTHIC FAUNAS OF FORESTED STREAMS AND SUGGESTIONS FOR THEIR MANAGEMENT

INTRODUCTION

All stream ecosystems are dependent on the surrounding terrestrial environment for a continuing supply of energy and nutrients in the form of dissolved and particulate organic matter. The surrounding catchment therefore can be expected to have a major influence on the nature and functioning of the stream ecosystem or to quote Hynes (1975) "... in every respect the valley rules the stream.... We must, in fact, not divorce the stream from its valley in our thoughts at any time. If we do, we lose touch with reality." Given this situation, a potential conflict of interest between forestry and stream conservation is apparent.

In 1963, Ross hypothesised that certain North American Trichoptera (caddisflies) were "confined to distinctive terrestrial biomes" in response to the physical and biological influences of the local vegetation on the stream bed and, subsequently, much research has been conducted to clarify the links between forest and stream ecosystems (Fisher & Likens, 1973; Hynes, 1975; Meehan *et al.*, 1977; Swanson *et al.*, 1976). In particular, continuing work in the Coast and Cascade Ranges of Oregon (Meehan *et al.*, 1977) and at Hubbard Brook, New Hampshire (see Likens *et al.*, 1977) has been invaluable in detailing terrestrial-stream ecosystem linkages and raising the general consciousness of parties involved in making forest management policy decisions.

Research being carried out by the New Zealand Forest Service at Maimai and Big Bush is providing information on the effects of logging practices on hydrology, sediment loads and water chemistry of streams draining small beech forest catchments (e.g., Pearce *et al.*, 1976; Neary *et al.*, 1978; O'Loughlin *et al.*, 1980). However, critical assessment of forestry practices on stream faunas is lacking in this country. Only Graynoth (1978, 1979) has really addressed this question and his study of Donald Creek (1979) is too limited, both taxonomically and in scope, to have general applicability for management.

Before impacts of forestry practices on stream faunas can be assessed adequately, it is important that the nature of faunas in undisturbed forest streams be known. No extensive comparative surveys of stream communities in relation to forest and other vegetational types have been made in New Zealand and the influence of physical factors (e.g., flow, substrate size, stability) on invertebrate distributions is poorly understood (Winterbourn, 1981). In order to partly rectify this situation I carried out surveys in 43 first to third

order streams in a variety of indigenous forest types and exotic pine plantation in the three main islands of New Zealand.

At each site, the benthic invertebrate fauna was sampled and selected physical characteristics of the catchment, stream bed and adjacent banks recorded. So that objective comparisons of physical characteristics could be made, a survey procedure developed by Pfankuch (1975) to measure stream stability in the U.S.A. was used.

MATERIALS AND METHODS

Forty-three streams in wholly or partially forested catchments were selected as study sites (Figure 5.1). Sites were chosen either by perusing local topographic maps for potentially suitable streams or by direct investigation of promising regions. Only streams bordered by riparian vegetation were selected and most sites were narrow (an active channel of <6 m wide at sampling), well shaded reaches about 30 m long. Streams were sampled at various times of year with each stream being sampled once.

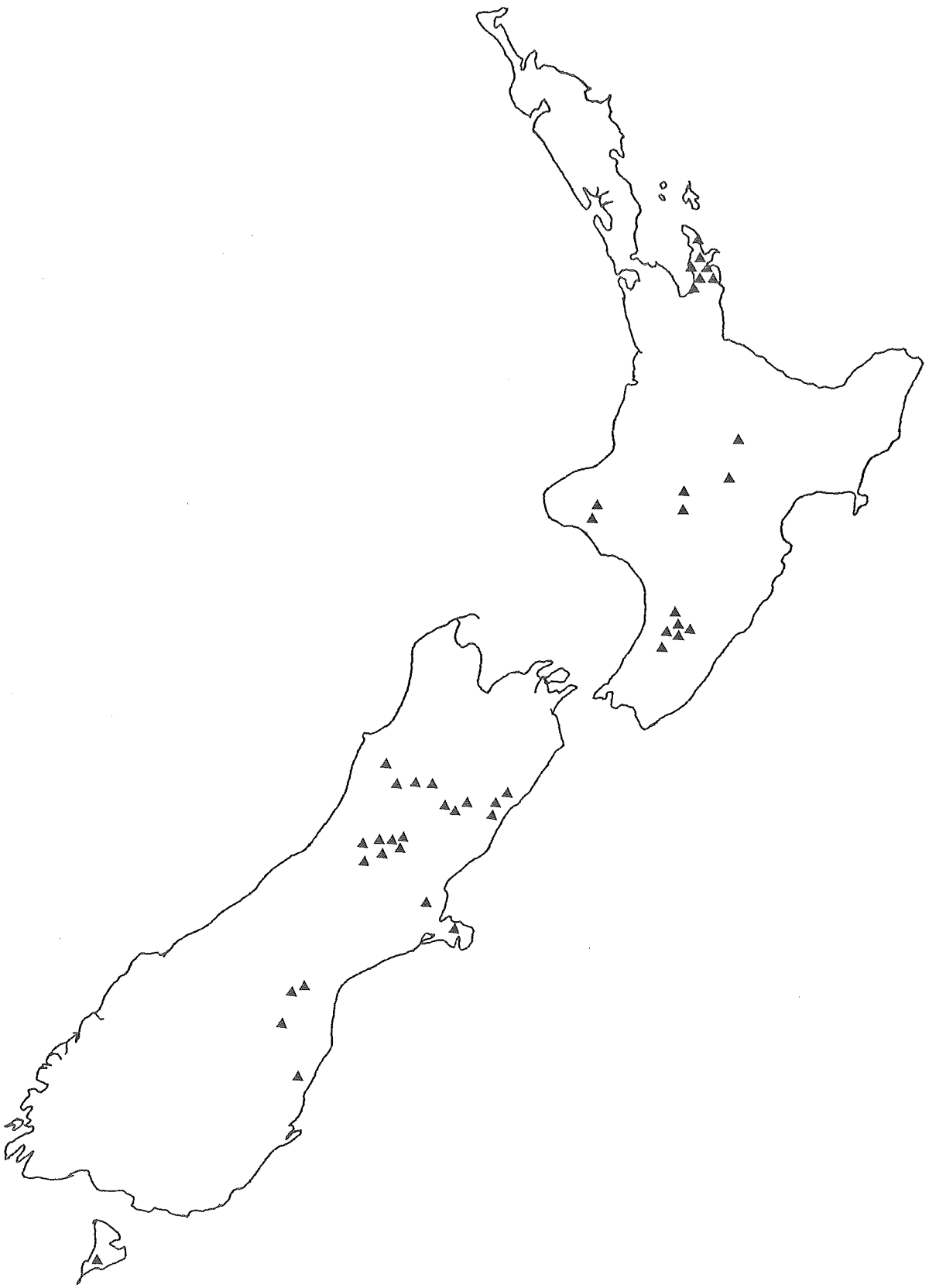
Streams were classified according to forest type as exotic (pine plantations), beech, podocarp-hardwood-beech, or podocarp-hardwood. This follows the scheme used by Wendelken (1976) except that his kauri-podocarp-hardwood category is included with other podocarp-hardwoods.

In the South Island, forests classified as beech occur predominantly east of the main alpine divide and even alongside streams few tree species other than *Nothofagus* occur (Burrows, 1977). On the other hand, in podocarp-hardwood-beech forests deciduous fuchsia (*Fuchsia excorticata*) and wineberry (*Aristotelia serrata*) may occur along stream banks and contribute pulsed, allochthonous inputs (Cowie, 1980).

The podocarp-hardwood group encompasses a greater diversity of trees including species of Podocarpaceae (softwood timber trees such as matai (*Podocarpus spicatus*) and totara (*P. totara*), many kinds of "broadleaf" hardwood trees (e.g., kamahi (*Weinmannia racemosa*), tawa (*Beilschmiedia tawa*) and mahoe (*Melicytus ramiflorus*) and an abundance of shrubs, ferns, tree-ferns, epiphytes and lianes.

Physical parameters were recorded first. Channel gradient was measured with an Abney level, stream width with a metric tape and pertinent observations on stream bed structure, catchment conditions

Figure 5.1 Locations of the 43 streams surveyed.



and degree of shading noted. A survey designed by Pfankuch (1975) to evaluate channel stability was then carried out. The Pfankuch survey is a systemised procedure in which a series of physical factors are examined and given numerical scores. Upon summing the individual scores an overall stream rating is obtained and this can be translated into one of four subjective categories: excellent, good, fair or poor. The stream rating represents a summary of "the resistive capacity of stream channels to the detachment of bed and bank materials and provides information about the capacity of streams to adjust and recover from potential changes in flow and/or in increases in sediment production" (Pfankuch, 1975).

Use of this survey technique requires judgment which is obtained by practice and through a thorough understanding of the criteria outlined in the survey guide (Pfankuch, 1975). In particular, it was important to consider the entire (approx. 30 m) reach in making judgments and to avoid keying in on one or a few indicators. As indicators are inter-related, over and under ratings tend to balance out as pointed out by Pfankuch (1975). In practice, the stream channel is divided into three components, upper banks, lower banks and channel bottom (Figure 5.2), so as to focus the surveyor's attention on particular indicators which are to be evaluated (see Table 5.1 in which a sample survey form is given).

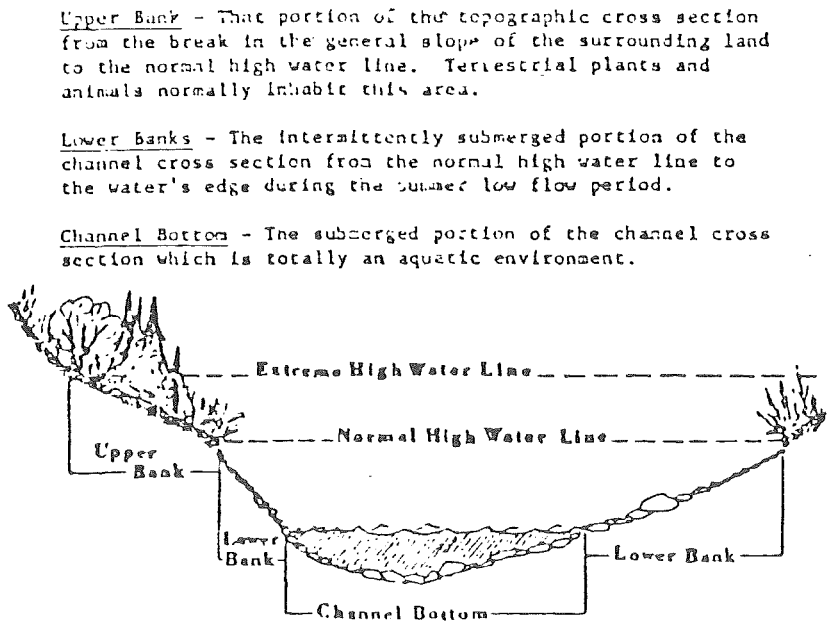


Figure 5.2 Illustration of stream channel areas which are used in physical surveys (from Pfankuch, 1975).

Table 5.1 A sample survey form from Pfankuch (1975).

STREAM CHANNEL STABILITY FIELD EVALUATION FORM

Item Rated	Stability Indicators by Classes							
Upper banks	EXCELLENT		GOOD		FAIR		POOR	
Landform slope	Bank slope gradient <30%	(20)	Bank slope gradient 30-40%	(4)	Bank slope gradient 40-60%	(6)	Bank slope gradient 60%+	(8)
Mass-wasting (existing or potential)	No evidence of past or any potential for future mass-wasting into channel.	(3)	Infrequent and/or very small. Mostly healed over. Low future potential.	(6)	Moderate frequency and size, with some raw spots eroded by water during high flows.	(9)	Frequent or large, causing sediment nearly year-long OR imminent danger of same.	(12)
Debris jam potential (floatable objects)	Essentially absent from immediate channel area.	(2)	Present but mostly small twigs and limbs.	(4)	Present, volume and size are both increasing.	(6)	Moderate to heavy amounts, predominantly larger sizes.	(8)
Vegetative bank protection	90%+ plant density. Vigor and variety suggests a deep, dense, soil binding root mass.	(3)	70-90% density. Fewer plant species or lower vigor suggests a less dense or deep root mass.	(6)	50-70% density. Lower vigor and still fewer species form a somewhat shallow and discontinuous root mass.	(9)	<50% density plus fewer species and less vigor indicate poor, discontinuous and shallow root mass.	(12)
Channel capacity	Ample for present plus some increases. Peak flows contained. W/D ratio <7.	(1)	Adequate. Overbank flows rare. Width to Depth (W/D) ratio 8 to 15.	(2)	Barely contains present peaks. Occasional overbank floods. W/D ratio 15 to 25.	(3)	Inadequate. Overbank flows common. W/D ratio >25.	(4)
Lower banks								
Bank rock content	65%+ with large, angular boulders 12"+ numerous.	(2)	40 to 65%, mostly small boulders to cobbles 6-12".	(4)	20 to 40%, with most in the 3-6" diameter class.	(6)	<20% rock fragments of gravel sizes, 1-3" or less.	(8)
Obstructions Flow deflectors Sediment traps	Rocks and old logs firmly embedded. Flow pattern without cutting or deposition. Pools and riffles stable.	(2)	Some present, causing erosive cross currents and minor pool filling. Obstructions and deflectors newer and less firm.	(4)	Moderately frequent, moderately unstable obstructions and deflectors move with high water causing bank cutting and filling of pools.	(6)	Frequent obstructions and deflectors cause bank erosion year-long. Sediment traps full, channel migration occurring.	(8)
Cutting	Little or none evident. Infrequent raw banks less than 6" high generally.	(4)	Some, intermittently at outcurves and constrictions. Raw banks may be up to 12".	(6)	Significant. Cuts 12-24" high. Root mat overhangs and sloughing evident.	(12)	Almost continuous cuts, some over 24" high. Failure of overhangs frequent.	(16)
Deposition	Little or no enlargement of channel or point bars.	(4)	Some new increase in bar formation, mostly from coarse gravels.	(8)	Moderate deposition of new gravel and coarse sand on old and some new bars.	(12)	Extensive deposits of predominantly fine particles. Accelerated bar development.	(16)
Bottom								
Rock angularity	Sharp edges and corners, plane surfaces roughened.	(1)	Rounded corners and edges, surfaces smooth and flat.	(2)	Corners and edges well rounded in two dimensions.	(3)	Well rounded in all dimensions, surfaces smooth.	(4)
Brightness	Surfaces dull, darkened or stained. Gen. not "bright".	(1)	Mostly dull, but may have up to 35% bright surfaces.	(2)	Mixture, 50-50% dull and bright, ±15%, i.e. 35-65%.	(3)	Predominantly bright, 65%+, exposed or scoured surfaces.	(4)
Consolidation or particle packing	Assorted sizes tightly packed and/or overlapping.	(2)	Moderately packed with some overlapping.	(4)	Mostly a loose assortment with no apparent overlap.	(6)	No packing evident. Loose assortment, easily moved.	(8)
Bottom size distribution and percent stable materials	No change in sizes evident. Stable materials 80-100%.	(4)	Distribution shift slight. Stable materials 50-80%.	(8)	Moderate change in sizes. Stable materials 20-50%.	(12)	Marked distribution change. Stable materials 0-20%.	(16)
Scouring and deposition	Less than 5% of the bottom affected by scouring and deposition.	(6)	5-30% affected. Scour at constrictions and where grades steepen. Some deposition in pools.	(12)	30-50% affected. Deposits and scour at obstructions, constrictions, and bends. Some filling of pools.	(18)	More than 50% of the bottom in a state of flux or change nearly year-long.	(24)
Clinging aquatic vegetation (moss and algae)	Abundant. Growth largely moss-like, dark green, perennial. In swift water too.	(1)	Common. Algal forms in low velocity and pool areas. Moss here too and swifter waters.	(2)	Present but spotty, mostly in backwater areas. Seasonal blooms make rocks slick.	(3)	Perennial types scarce or absent. Yellow-green, short term bloom may be present.	(4)
	COLUMN TOTALS							

Add the values in each column for a total reach score here (E___ + G___ + F___ + P___ = ___).

Reach score of: <38 = Excellent, 39-76 = Good, 77-114 = Fair, 115+ = Poor.

Survey repeatability was tested using several evaluators and found to be quite good. Thus, the total scores obtained by the experienced evaluators usually were within 5% of each other.

After the surveys had been completed benthic fauna was sampled by taking and washing the surfaces of displaced stones into a 1 mm mesh stream net. An attempt was made to collect from a wide variety of microhabitats within the surveyed reach. However, sampling intensity inevitably varied between sites because of different stream bed characteristics such as degree of substrate compaction, habitat accessibility etc. Collected invertebrates were preserved in 70% EtOH prior to sorting, counting and identification. Wherever possible invertebrates were identified to the species level but this is not possible for all New Zealand aquatic insects (Winterbourn & Gregson, 1981) and many could be identified only to genus or family. This was almost always the case with early instar larvae. Information lost through inability to discriminate between congeneric species may not be crucial in many groups however, as suggested by Wiggins & Mackay (1978) who argued that the genus can be considered as an ecological type or theme and that congeneric species are merely "subtle variations on this theme".

Because streams were sampled at various times of year, seasonal factors could be expected to account for some of the variation in invertebrate populations between sites. Many New Zealand stream insects have relatively non-seasonal life history patterns however, (Winterbourn, 1978b; Towns, 1981) and occur in streams as larvae throughout the year. Therefore, it is likely that collections made at any time are likely to include most, if not all, common species although their relative abundances may be affected. For this reason, and because sampling intensity varied between sites, the animal data do not lend themselves to sophisticated community analysis and this has been resisted.

RESULTS AND DISCUSSION

Faunal-Forest Associations

A list of the 43 streams, their location, physical characteristics, rating and faunal characteristics is presented in Appendix II*.

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* Footnote: A complete listing of the fauna collected at each site is on file with Dr M.J. Winterbourn, Zoology Department, University of Canterbury, Christchurch and is available upon request.

Sixty-one taxa of benthic invertebrates (excluding Chironomidae, which were not considered in the surveys) were identified from the 43 streams. These were predominantly aquatic insects (87%) of which Trichoptera (36% of total numbers), Plecoptera (13%) and Ephemeroptera (19%) were represented by most species.

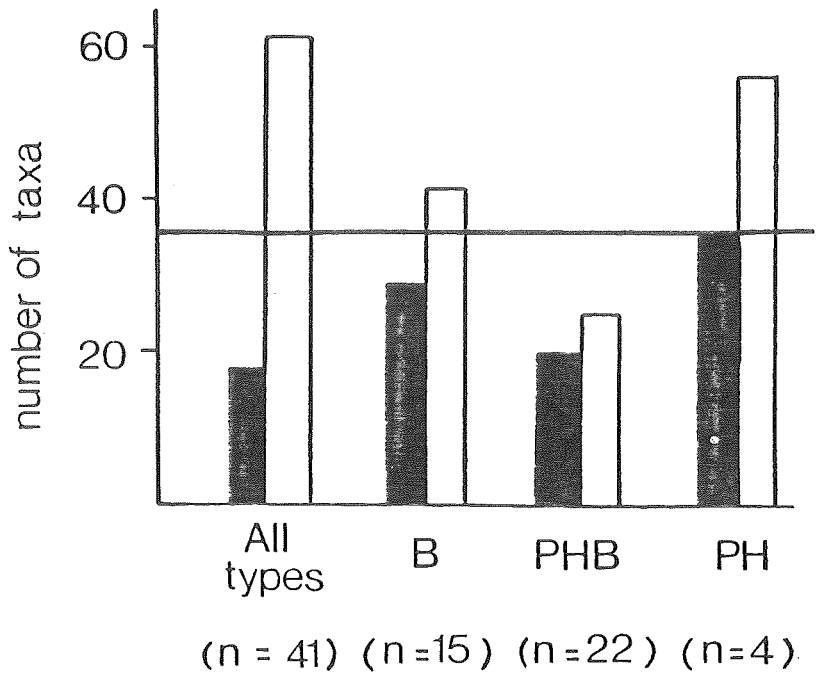
Twenty-four to 56 taxa were taken from streams in the three forest types (beech - 41 taxa; podocarp-hardwood-beech - 24; podocarp-hardwood - 56) considered (Figure 5.3) and a high percentage were held in common by all three types (Figure 5.4). No obvious relationship between invertebrate fauna and forest type was apparent. The lower numbers of taxa found in podocarp-hardwood-beech forest are probably a result of the fewer sampling sites located in that forest type (podocarp-hardwood-beech - n = 4; beech - n = 15; podocarp-hardwood - n = 22). Since only two streams in pine plantations were sampled they were not included in this comparison.

At each site, five taxa (not necessarily the same ones at each site - see Appendix II) accounted for a mean of 87.2% (range 66.7 - 100%) of the total fauna collected. Ubiquitous was the leptophlebiid mayfly, *Deleatidium* which was found in 42 of the 43 surveyed sites (Table 5.2). *Deleatidium* was a member of the top-5 in all 42 streams and was the most abundant invertebrate at 27 of these 42 sites. Other invertebrates which were widespread and abundant were the ephemeropterans *Nesameletus* and *Coloburiscus*, the plecopterans *Stenoperla*, *Zelandoperla* and *Zelandobius* and the trichopterans *Olinga* and *Hydrobiosis*. These nine genera occupied 114 of the 207 possible top-5 positions and represent a core element in New Zealand fauna. *Deleatidium*, *Olinga* and *Nesameletus* also were the most abundant species found in the two pine plantation streams surveyed. When top-5 taxa are compared with respect to forest type, the lack of specialised, forest-associated faunas is clear (Figure 5.4). Of the 35 taxa which occurred in the top-5, 18 were found in all forest types, 29 in beech, 20 in podocarp-hardwood-beech and 35 in podocarp-hardwood.

The presence of such a "universal" core fauna in very different types of forest streams is in contrast with suggestions of North American workers that close linkages exist between vegetation type and invertebrate community structure. This idea, often credited in the first place to Ross (1963), nevertheless has not been thoroughly tested and a number of workers (e.g., Cummins, 1974; Boling *et al.*, 1975; Malmqvist *et al.*, 1978) have overstated or misinterpreted Ross's initial claim. This was

Figure 5.3 Number of invertebrate taxa in all three forest types. Black histograms - taxa in top-5 abundance group (35 in total, horizontal line). Open histograms - all taxa. Forest types: B - beech; PHB - podocarp-hardwood-beech; PH - podocarp-hardwood.

Figure 5.4 The percentage of invertebrate taxa common to all forest types and to all possible pairs. Black histograms - taxa in the top-5 abundance group. Open histograms - all taxa. Forest types - as in Figure 5.3.


number of taxa
60
40
20
All types
B
PHB
PH
(n = 41)
(n =15)
(n =22)
(n=4)

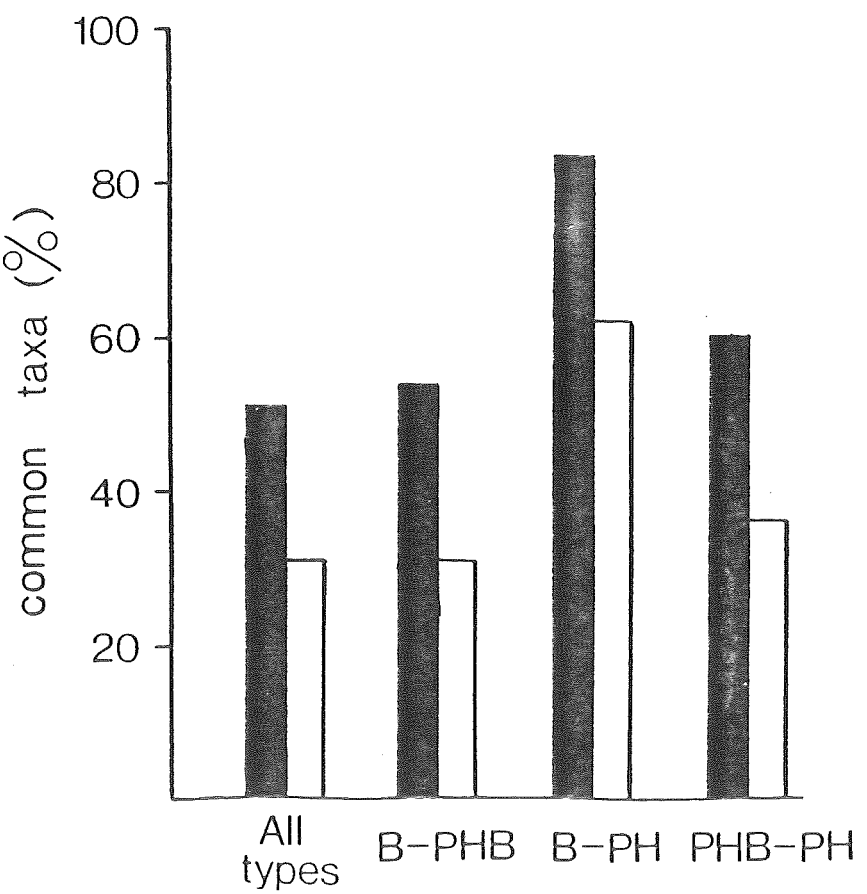

common taxa (%)
100
80
60
40
20
All types
B-PHB
B-PH
PHB-PH

Table 5.2 Number of occurrences and top-5 placings of taxa which occurred at least once in the top-5 abundance group.

	Total no. of occurrences	Times in Top-5	Top-5 Placing				
			1st	2nd	3rd	4th	5th
Ephemeroptera							
Deleatidium	42	42	27	9	2	3	1
Nesameletus	19	9	0	5	2	0	2
Coloburiscus humeralis	22	18	7	3	3	4	1
Arachnocolus phillipsi	2	1	0	1	0	0	0
Plecoptera							
Stenoperla prasina	27	12	0	1	3	4	4
Zelandoperla	16	9	1	2	2	1	3
Spaniocerca zelandica	8	6	1	2	1	0	2
Zelandobius	14	6	0	0	3	1	2
Austroperla cyrene	11	3	0	0	1	0	2
Megaleptoperla grandis	6	1	0	0	0	1	0
Trichoptera							
Olinga feredayi	20	14	0	4	4	5	1
Oeconesidae	10	9	3	0	1	3	2
Orthopsyche	10	8	0	1	4	1	2
Aoteapsyche	13	7	0	4	1	1	1
Hydrobiosella	10	4	1	1	1	1	0
Hydrobiosis	18	4	0	1	0	3	0
Helicopsyche	7	2	1	0	1	0	0
Philorheithrus agilis	8	2	0	0	1	0	1
Costachorema	6	1	0	0	0	1	0
Polyplectropus	3	1	0	0	0	0	1
Psilochorema	13	1	0	0	0	1	0
Pycnocentria	6	1	0	0	1	0	0
Pycnocentrodes	4	1	0	0	1	0	0
Triplectides obsoleta	6	1	1	0	0	0	0
Coleoptera							
Elmidae	18	12	0	5	2	3	2
Helodidae	4	1	0	0	0	0	1
Ptilodactylidae	6	2	0	0	0	2	0
Diptera							
Austrosimulium	4	1	0	0	0	1	0
Aphrophila neozelandica	4	2	0	0	0	0	2
Other Tipulidae	16	4	0	0	3	0	1
Oligochaeta							
Eiseniella tetraedra	6	3	0	1	0	0	2
Decapoda							
Paranephrops	5	5	0	1	0	3	1
Megaloptera							
Archichauliodes diversus	20	9	1	0	3	2	3
Gastropoda							
Potamopyrgus antipodarum	8	1	0	0	1	0	0
Amphipoda	6	3	1	0	1	0	0

that a "correlation which appears too great to be accidental" is found between the distribution of many species groups and genera of caddisflies and the terrestrial biomes or landscape aspect areas. In particular, certain aspects of the forest might be controlling this pattern through dense shading, maintaining cool stream temperatures, etc. Recent work at Oregon State has emphasised the role of riparian vegetation as a major controller of habitat and community structure in small and intermediate sized streams (see Meehan *et al.*, 1977). Current research proposals from that institution (S.V. Gregory, Oregon State University, pers. comm.) even go so far as to suggest that as "features of riparian vegetation can be determined from aerial photography, the proposed relationships (between riparian vegetation and benthic community structure) hold the potential for a remote procedure to predict existing and future stream community structure and function". No evidence for a strong relationship between benthic fauna and riparian forest vegetation type is apparent in New Zealand and the question remains, is the North American claim a popular misconception?

Stream Geomorphology - Faunal Relationships

Pfankuch ratings of streams surveyed in this study ranged from 41 to 147 with a mean of 96 (S.D. = 26). This mean falls into the middle of the category described subjectively as "fair". No New Zealand streams rated excellent and only 12 of the 43 sites were categorised as "good".

Lotic invertebrates apparently respond more strongly to physical stream parameters than to forest types and numbers of taxa collected were negatively correlated ($r = -0.41$, $p < 0.01$) with the Pfankuch rating; i.e., in general, more taxa were present in the more stable streams. This is in agreement with Cowie's (1980) findings for a West Coast forest stream system and is probably a result of more stable streams offering a greater variety and constancy of habitats and food resources.

Distribution of Shredders

Because they can play an important role in organic matter processing elsewhere (Cummins, 1974) and because their apparent scarcity in New Zealand streams has puzzled ecologists, the distribution of shredders (leaf-feeding insects) was examined in relation to stream gradient and stability. Streams were classified with respect to shredder abundance as follows: (1) absent, (2) present - shredders 0.1 to 3.0% of the fauna, (3) abundant - shredders greater than 3.0% of the total faunal numbers.

Shredder abundance was not correlated with stream gradient ($r = 0.16$) which might have been expected to affect retention of organic matter. Shredder abundance was correlated significantly with Pfankuch stability rating however ($r = -0.61$, $p < 0.01$, $n = 43$), and most streams which scored over 100 lacked shredders. On the other hand, streams which scored less than 100 had resident (if small) shredder populations.

Comparative studies in two beech forest streams of contrasting stability (Middle Bush Stream, score 90; Craigieburn Cutting, score 110) indicated that organic matter retention was a major factor controlling shredder distribution. Stability ratings can be seen as providing a measure of this factor.

Suggestions for Management of N.Z. Stream Ecosystems in Relation to Forestry Practices

The first step in deciding upon appropriate management practices is to determine what goals need to be met. With respect to forest-stream ecosystem management, a reasonable overall aim would seem to be to ensure that ecosystem functioning remains essentially unaltered as a result of forestry practices. Maintenance of unchanged benthic invertebrate communities (in the taxonomic sense) need not be of prime concern, since many species play equivalent roles in an ecosystem context and losses or gains of particular species may be of little consequence in functional terms.

Further, the presence in New Zealand of a common, widely distributed core fauna regardless of forest type suggests that few (if any) species are dependent on particular types of terrestrial vegetation and conversion from indigenous to exotic forest *per se* appears to have little impact on the nature of stream invertebrate communities.

The removal of stream-side vegetation has two obvious effects on streams:

(1) The stream bed is opened up, resulting in its exposure to higher light intensities.

(2) Rates of sediment and, frequently, nutrient input increase.

Opening up of the canopy can result in increasing aquatic production at all trophic levels (Murphy *et al.*, 1981) which also may be stimulated by

increased nutrient levels (Borman *et al.*, 1968; O'Loughlin *et al.*, 1980). Murphy *et al.* (1981) demonstrated a clear relationship between increased light levels and increases in primary production, microbial respiration, invertebrate and vertebrate production. How permanent such increased productivity will be is another matter, however, and will depend largely on patterns of regrowth (see Murphy & Hall, 1981).

The effects of canopy change (forested to open) on faunal composition has been investigated both overseas and in New Zealand. Overseas work (e.g., Erman *et al.*, 1977; Webster & Patten, 1979; Newbold *et al.*, 1980) has demonstrated marked changes in stream faunal composition particularly in catchments which have been logged without a buffer strip being left intact. This is in contrast to the local situation where observations on the nature of New Zealand stream faunas in general (Winterbourn *et al.*, 1981) indicate that a nucleus of common genera and species prevail in many streams whether they be in native beech, podocarp-hardwood forest, pine plantations or even grasslands (Table 5.3). Many of these species clearly possess wide ecological flexibility with respect to habitat requirements, life history patterns and food requirements (see Chapter IV).

Sedimentation, unlike canopy opening, results in reduced productivity and has long been recognised as a problem associated with logging practices (see Iwamoto *et al.*, 1968; Griffiths & Walton, 1978). Forest vegetation plays a key role in stabilising slopes and reducing erosion and, when it is lost, increasing quantities of sediment and soil may wash into streams often with disastrous effects (e.g., Tebo, 1955; Cordone & Kelly, 1961; Hynes, 1973). Roads, tracks and landings have been identified as prime sources of sediments which enter streams as a result of either fluvial erosion or mass-wasting processes (Dyrness, 1967; Swanston & Swanson, 1976; O'Loughlin *et al.*, 1980). For this reason, they should be carefully sited so as to minimise possible sedimentation problems.

Buffer strips, stands of vegetation left intact along stream banks, have been advocated as a means of protecting streams from logging impacts (Newbold *et al.*, 1980) and several studies have shown that they are effective for ensuring that no decline in fish populations occurs (e.g., Hall & Lantz, 1969), controlling stream temperature (Brazier & Brown, 1973), and sediment flows (Haupt & Kidd, 1965; Meehan *et al.*, 1977). In New Zealand, where direct forest vegetation-stream invertebrate linkages appear to be weak, it is probable that buffer strips are primarily of value as "policemen" (Moring, 1975; Newbold *et al.*, 1980) limiting direct

Table 5.3 Representation of top-5 taxa in three non-forested New Zealand streams. + = present, ++ = most common.

Stream	Whaeo River	Hinau Stream	Kowhai River
Reference	NZ Wildlife Service (unpubl.)	Hopkins (1976)	S.F. Davis (unpubl.)
Location	Central North Island	Southern North Island	Inland Canterbury
Dominant Vegetation	Pine plantation	Broadleaf forest scrub, pasture	Tussock grassland
Ephemeroptera			
Deleatidium	++	++	++
Nesameletus	+	+	++
Coloburiscus	+	+	
Plecoptera			
Zelandoperla	+	+	+
Zelandobius	+	+	++
Spaniocerca			+
Stenoperla		+	+
Austroperla	+	+	
Megaleptoperla	+		
Megaloptera			
Archichauliodes	+	+	+
Coleoptera			
Elmidae		+	+
Trichoptera			
Aoteapsyche	+	+	+
Orthopsyche	+	+	
Polyplectropus	+		+
Hydrobiosella		+	
Hydrobiosis	+	+	+
Psilochorema	+	+	+
Pycnocentria	++	+	
Olinga	++	+	+
Pycnocentrodes		+	
Oeconesidae	+	+	
Philorheithrus			+
Helicopsyche		++	
Triplectides			
Gastropoda			
Potamopyrgus	+	++	
Total listed genera	18	22	15

sediment introduction and protecting stream banks from logging-induced erosion.

Physical and faunal surveys of the kind described here (carried out in conjunction) have the potential to identify streams which may require particular protection. That is, they can point out potential trouble spots. For example, the communities in relatively stable streams (those with low Pfankuch scores) are likely to be subject to relatively greater disturbance than those in unstable streams since shredders' foods would be lost (riparian vegetation) and inputs of sediment would reduce habitat stability and heterogeneity.

On the other hand, in naturally unstable streams shredders will already be absent and it is probable that only "common core" species occur. In such situations, forestry practices should have little effect on stream fauna, providing severe sedimentation is prevented.

New Zealand needs local management plans developed from local information. A survey technique such as this is the first step in assuring that both forestry and aquatic preservation goals become more compatible.

CHAPTER VI

ARE NEW ZEALAND STREAM ECOSYSTEMS REALLY DIFFERENT?

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Discussion paper*

Are New Zealand stream ecosystems really different?

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Abstract New Zealand stream ecosystems differ from many of their North American counterparts, on which general stream ecosystem models are based, in several ways. In New Zealand, large particle detritivores (shredders) are poorly represented, and the dominant invertebrates are browsers which feed on fine particulate organic matter and stone-surface organic layers. In contrast with the river continuum concept of Vannote et al. (*Canadian Journal of Fisheries and Aquatic Sciences 37*: 130–137, 1980), representation of functional feeding groups shows little change downstream and a temporal continuum of synchronous species replacements is not found. Many common benthic invertebrates are ecologically flexible species with poorly synchronised life histories. These differences appear to be associated with the non-retentive, climatically unpredictable nature of the stream environment. The idea that stream communities are highly structured entities is questioned, as is the generality of the river continuum concept.

Keywords stream ecosystems; river continuum concept; ecology; functional feeding groups; organic layers.

INTRODUCTION

The river continuum concept of Vannote et al. (1980) has focussed attention on stream ecosystems as predictably organised units, and attempts to provide a conceptual framework of their organisation. It extends the idea that streams possess assemblages of species, which respond to physical gradients, to include functional relationships. Community structure and function are seen as adjusting to changes in certain geomorphic, physical, and biotic variables, such as stream flow, channel morphology, detritus loading, size of particulate organic material, characteristics of autotrophic production, and thermal regime, to achieve a state of dynamic equilibrium. Since downstream communities are considered to be dependent on those upstream for at least part of their energy income, Vannote et al. (1980) hypothesised that they will become structured in a predictable manner to utilise this material most efficiently.

Although it is based primarily on North American experience, Vannote et al. inferred that their model is a universal one and, therefore, by implication applicable to New Zealand river systems. The results of our studies and those of colleagues in this country are at odds with several specific criteria of the river continuum concept, and have led us to ask the question: Are New Zealand stream ecosystems really different? If they are, why should this be so, and if not, is there something wrong with the North American model?

Since the river continuum concept has attempted to draw together many of the recent developments in stream ecology, it is appropriate for us to consider New Zealand streams in its light.

NEW ZEALAND STREAM ECOSYSTEMS

Physical background

New Zealand is a small country with a complex, diverse landscape including prominent mountain ranges. Peaks in the Southern Alps range up to 3764 m (Mt Cook), and although they are lower in the North Island (maximum 2797 m, Mt Ruapehu), they offer much steep, finely dissected relief. In common with other Southern Hemisphere land masses the timber line is low (1200–1500 m), and consequently extensive river catchments occur above the forests in terrain which is often steep and barren. Scree slopes are a continual source of the sediments carried down mountain streams and may be a striking feature of the landscape, as in the Cass–Arthur's Pass region of the South Island. Since heavy rainfalls occur

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*Comments, brief and to the point, are welcomed by the Editor and may be published as "Letters to the Editor". The authors of the Discussion Paper will be given the right of reply

unpredictably and frequently in mountainous areas, it is not surprising that sediment yields measured in several New Zealand rivers are among the highest reported in the world (Griffiths 1979).

River continua in New Zealand are short, with major rivers having a stream order (sensu Strahler (1957)) of only 6 or 7 compared with 12 for a long river like the Mississippi. Mountain streams typically are turbulent and fast-flowing with shifting and unstable beds and poor debris retention characteristics. The extensive, evergreen beech and podocarp–hardwood forests, often with poorly developed subcanopy vegetation (notably in beech forests), and a paucity of deciduous, riparian trees, provide streams with only small quantities of woody debris compared with many elsewhere. Thus, in New Zealand it is rare for more than 5–10% of forest stream beds to hold wood debris, whereas in parts of western North America it is common for up to 50% of stream bed area to be covered with wood and associated materials (Sedell & Triska 1977) and debris dams can remain intact for over 100 years (Swanson et al. 1976).

Where they pass through foothills and over plains, many New Zealand rivers, particularly in the South Island, have extensive braided channels and gravel beds which may be dry at the surface in summer and muddy torrents after heavy rain or snowmelt. Not all our rivers are as physically imposing as this, however, but unfortunately, from the point of view of this discussion, many of the smaller, lower gradient streams and rivers now drain agricultural and urban catchments and are subject to varying degrees of enrichment or other modification. This brief description has stressed the instability and unpredictability of New Zealand stream environments, features which must be kept clearly in mind when trying to understand the nature of their biological communities.

Characteristics of the invertebrate fauna

At the higher taxonomic levels (family or subfamily and above), New Zealand stream faunas show numerous differences from their Northern Hemisphere counterparts, although in some groups (e.g., Oligochaeta) there is a predominance of cosmopolitan species. The dominant mayflies are Leptophlebiidae and Siphlonuridae, and the best represented stoneflies are Gripopterygidae and Notonemouridae. Large stoneflies equivalent to the familiar perlids, perlodids, and pteronarcids of the Northern Hemisphere are poorly represented. Chironomidae and to a lesser extent Tipulidae and Simuliidae are the most abundant lotic Diptera, and Elmidae, Hydraenidae, and Helodidae are the commonest beetles. Several other groups typically associated with running waters have few representatives in New Zealand; thus there is only one megalopteran (a corydalid), and very few Odonata, Gastropoda, or Crustacea. In contrast, caddisflies are well represented in New Zealand's running waters, but like the stoneflies most are rather small. Species of Conoesucidae, Hydropsychidae, Rhyacophilidae (Hydrobiosinae), and Hydroptilidae are best represented, and apart from a few species of Oeconesidae and Leptoceridae whose larvae are typical shredders there are no ecological equivalents of the Northern Hemisphere Limnephilidae, Lepidostomatidae, and Odontoceridae, or of the algal-scraping Glossosomatidae.

Benthic invertebrate communities

Throughout New Zealand, unmodified streams tend to have remarkably similar faunas with a nucleus of common genera (*Deleatidium, Coloburiscus, Nesameletus* (Ephemeroptera); *Stenoperla, Zelandoperla, Zelandobius* (Plecoptera); *Hydrobiosis, Psilochorema, Pycnocentria, Olinga, Aoteapsyche* (Trichoptera); *Archichauliodes* (Megaloptera); *Potamopyrgus* (Gastropoda)) and species. This faunal similarity extends to streams in exotic plantations as well as in native forest and grassland, a point of significance for stream management and one that is contrary to the appealing idea that stream insects may show close adaptation to forest vegetation. Although frequently mentioned, this is an unresolved issue, and a careful reading of Ross (1963), the authority most frequently cited in this respect, shows that many of the statements attributed to him exaggerate his suggestion that "the forest itself superimposes certain ecological conditions upon the streams originating in it and running through it, ecological conditions necessary for the survival of the caddisflies."

Changes in community structure along unperturbed montane streams in New Zealand appear to be related primarily to physical factors, especially stream size, slope, and stability, and secondarily to the nature of the energy sources available to the fauna (Cowie 1980). Highly unstable stream beds may support a diverse insect fauna, but our work suggests that the most diverse faunas are associated with the more stable stream channels exhibiting a high degree of substrate heterogeneity. This is in accordance with Minckley's (1963) contention (expanded by Bishop (1973)) that increasing heterogeneity promotes faunal diversity, but is contrary to the suggestion of Vannote et al. (1980) that physical stability may be equated with low diversity. Cowie's (1980) work on West Coast streams also showed that although severe floods were frequent and temporally unpredictable, they had little apparent effect on species richness or

relative abundance at his more stable sites. Perhaps this is not surprising given the climatic and physiographic conditions prevailing in New Zealand.

Winterbourn (1976) and Davis & Winterbourn (1977) suggested that species diversity in New Zealand streams is poor compared with that found in many streams elsewhere, but the comprehensive studies of Towns (1976) and Cowie (1980), in kauri and beech forest streams respectively, indicated that this is not necessarily so. Nevertheless, it is true that several major faunal groups have only a few common species whose distributions show that they have broad ecological requirements. Amongst the Ephemeroptera and Plecoptera, for example, the one or two species of *Coloburiscus, Nesameletus, Stenoperla,* and *Spaniocerca* are widely distributed and often abundant in different kinds of rivers and streams. On the other hand, considerable diversity is shown by Trichoptera (notably Rhyacophilidae and Hydropsychidae) and Diptera, orders possessing holometabolous development which might be expected to have aided in the evolution of more precise larval adaptation to specific habitats. Despite this radiation, differences in ecological niches of related or potentially competitive species have proved difficult to define (Devonport & Winterbourn 1976, Winterbourn 1978b), although some rhyacophilids show altitudinal distribution patterns (McFarlane 1938) and some species of Hydropsychidae, Oeconesidae, Rhyacophilidae, and Calocidae are restricted either to open or forested streams.

Larvae of most New Zealand aquatic insects also show little evidence of food specialisation. Carnivorous species examined (*Stenoperla, Archichauliodes, Polyplectropus, Hudsonema, Microchorista,* several Rhyacophilidae) appear to be generalists taking suitably sized prey more or less in proportion to its abundance and availability (Winterbourn 1974, 1978b, Crosby 1975, Devonport & Winterbourn 1976, authors' unpubl. data), while most browsers are also food generalists, feeding predominantly on fine particulate organic matter and the organic layers present on the surfaces of stones (see below). There is little evidence of food partitioning, and several surface-browsing stoneflies and caddis (species of *Spaniocerca, Zelandobius, Zelandoperla, Olinga*) can act as opportunistic shredders (Davis & Winterbourn 1977, Cowie 1980). Similarly, all New Zealand Hydropsychidae appear to construct similar nets which capture a mixture of detrital and animal foods, whereas in many other parts of the world it seems to be common for species to partition food resources through the use of nets differing in mesh size (Wallace 1975).

In addition to their broad habitat requirements and apparent lack of feeding niche differentiation, many New Zealand stream insects possess flexible, poorly synchronised life histories (Winterbourn 1978a, Towns 1981). These can vary in the length of the larval period (e.g., 1–3 years in *Stenoperla prasina* (Cowie 1980)), exhibit non-seasonal or weakly seasonal patterns of development, and include extended flight and egg-hatching periods. Temporal segregation of taxonomically or functionally related species through staggering of their development and emergence periods as described by Mackay (1969), Kerst & Anderson (1974), Vannote & Sweeney (1980), and others in North America does not occur. This contrasts with the contention of Vannote et al. (1980) that the biological communities of natural streams should incorporate a temporal continuum of synchronised species replacements associated with seasonal variations in the nature of the food base, thereby enabling the efficient utilisation of inputs over time. Instead, because of their broad, ecological flexibility, e.g, possession of wide ecological niches, single New Zealand species appear to be functionally equivalent to several sequentially appearing North American species. Whether this implies that seasonal variations in the nature of energy inputs and physical conditions are minimal, as the argument of Vannote et al. (1980) suggests, is an interesting point which is touched upon below. Regardless of this, it is our belief that abiotic factors have been of paramount importance in shaping the nature of New Zealand stream communities. In particular, the prevalence of steep, unstable streams and the unpredictability of the physical environment appear to have favoured selection for opportunism, while the risks of unseasonal insect emergence or larval cohort losses have been spread by the evolution (or maintenance of what may be the primitive, generalised condition) of poorly synchronised life histories.

STREAMS AS ECOSYSTEMS

The importance of coarse particulate organic matter (CPOM) (principally autumn-shed leaves) as a major source of energy to small forest stream communities has been emphasised by North American stream ecologists (e.g., Cummins 1974), and numerous studies have focussed on the mechanisms of litter breakdown and decomposition (e.g., Petersen & Cummins 1974, Hart & Howmiller 1975, Padgett 1976, Triska & Sedell 1976, Davis & Winterbourn 1977, McCammon 1980). The role played by microorganisms in conditioning CPOM, thereby increasing its nutritive value and palatability to many detritivores, is also well established (Kaushik & Hynes 1971, Barlocher & Kendrick 1973, Cummins 1974, Iversen 1974). Hyphomycetous fungi appear to be the key colonists of dead leaves in many streams (Barlocher & Kendrick

Table 1 Percentage of New Zealand trichopteran genera in 4 functional feeding categories and a comparison with some overseas caddis faunas. Feeding categories of Northern Hemisphere and Chilean (in part) faunas based mainly on summaries by Merritt & Cummins (1978); where information not available we assigned genera to the trophic class of closely related genera. Placement of Tasmanian genera and southern element of Chilean fauna inferred from our knowledge of their New Zealand relatives.

Fauna	No. of genera	Percentage of				Source
		Shredders	Filterers (collectors)	Browsers	Predators	
New Zealand	41	12	12	44	32	Wise (1973)
South Island forest streams	26	15	8	38	38	Authors' studies
Tasmania	62	14	8	43	34	Neboiss (1977)
Chile	57	35	5	21	38	Flint (1974)
Eastern deciduous forest biome, North America	88	34	23	32	11	Wiggins & Mackay (1978)
Western montane forest biome, North America	59	37	15	37	10	Wiggins & Mackay (1978)
Northwestern Europe	86	35	10	31	10	Svensson & Tjeder (1975)

1975), although bacteria can also play this role, as on *Fagus* and *Nothofagus* leaves in Danish and New Zealand streams respectively (Iversen 1973, Davis & Winterbourn 1977).

Not surprisingly, recent discussions of stream ecosystem structure and function have emphasised the important role of shredders (CPOM feeders), an attitude summed up in Hynes's (1975) phrase that shredder feeding lay "at the base of almost all the biotic activity in the water".

In New Zealand, shredders are poorly represented in the fauna and frequently may be absent from forested headwater streams. Their relative scarcity is illustrated in Table 1, in which the feeding modes of larval Trichoptera (one of the principal orders containing shredders elsewhere) are analysed. In New Zealand and Tasmania—a land mass of similar climate and topography to New Zealand—only 12 and 14% of genera are classified as shredders compared with 34–37% in parts of North America and Europe. In Chile, much of whose fauna has strong phylogenetic links with those of southeastern Australia and New Zealand rather than the rest of South America (Flint 1974), the relatively high representation of shredders can be accounted for by the presence of Sericostomatidae (9 genera) and Limnephilidae (6 genera), northern families which are absent from New Zealand (although one limnephilid genus occurs in Tasmania). On the other hand, predators are overrepresented in Southern Hemisphere faunas, reflecting in large part the radiation of Hydrobiosinae (Rhyacophilidae) in New Zealand (9 genera), Tasmania (10 genera), and Chile (17 genera).

For shredders to occur, a stream must be able to retain CPOM, as often happens in small, low gradient tributaries where even in New Zealand shredders can be common (Graynoth 1979, authors' unpubl. data). Evidence that retention is of major significance was shown by our experiments with larvae of the caddisfly *Zelandopsyche ingens* which were caged for 3 months in an unretentive stream with no resident caddis population, yet survived and grew (utilising leaf litter from the recipient stream as food) as well as larvae kept under identical conditions within the donor stream. Peckarsky (1980) has suggested, and Young et al. (1978) have inferred, that shredders are essentially opportunistic species occurring where conditions allow. Clearly, this is so in New Zealand where they do not play a fundamental role in organic matter processing or energy flow in streams.

A fundamental part of the river continuum concept (Vannote et al. 1980) is that as one moves from headwaters to mouth, adjacent watershed vegetation will have a decreasing direct influence on the river ecosystem (an extension of the ideas of Ross (1963)), while detrital inputs from upstream tributaries and in situ algal production become increasingly important. The theory implies that downstream communities depend on upstream areas for a proportion of their energy in the form of fine particulate organic matter (FPOM), at least some of which is derived from CPOM through the feeding activities of shredders. Thus, Cummins (1975), in describing headwater streams as "CPOM-fungi-shredder–FPOM-bacteria-collector systems", implied that shredders were significant producers of collector food, Anderson & Cummins (1979) stated that "much of it [FPOM] is fecal material produced by shredders and other functional groups", and Short & Maslin (1977) contended that "shredders are of great importance ... with regard to nutrient

availability to the various collector species ". We would be surprised to find that FPOM of shredder origin was a major source of collector food, except perhaps in highly retentive headwater streams, and note that, despite their authoritative ring, surprisingly little evidence has been forthcoming to substantiate claims such as those quoted above.

The gut contents of insect larvae from the headwaters and lower reaches of a wide range of New Zealand rivers and streams indicate that FPOM is indeed the major particulate material ingested, but since shredder feeding is negligible it must have other origins. We suspect that much of this material (Table 2) enters our streams already in fine particulate form, via wind blow, surface runoff, and bank erosion, and suggest that such sources are also of considerable importance in many streams elsewhere. Since many New Zealand rivers begin in the mountains high above the tree line where typically eroded, windswept conditions prevail, it is likely that primary tributaries receive extensive fine particulate inputs, and at least seasonally may support considerable primary production. Even where shredders are conspicuous, as in Manson Creek (Table 2) or Middle Bush Stream, Cass (Winterbourn 1978a), it is most unlikely that they are the main source of FPOM ingested by insect larvae since the sizes and shapes of most particles found in insect guts are quite unlike those of faecal fragments produced by shredders inhabiting the streams. It might be argued that faecal fragments break down further before reingestion, but *Nothofagus* leaves (the main materials ingested in beech forest streams) are notably tough and lignified, and this seems inherently unlikely. In shallow gradient, non-forested streams, aquatic macrophytes and/or algae also may represent a major source of the FPOM ingested by benthic insects. However, since few if any of our stream-dwelling invertebrates eat living macrophyte tissue directly, animal feeding again cannot be of importance in FPOM production; therefore we presume that breakdown and decomposition occur primarily by microbial and mechanical means.

As well as being food items in their own right, fine particles also form an important component of the organic layers which occur on the surfaces of stones, logs, and leaves in streams (Madsen 1972, Calow 1975, Pennak 1977). Traditionally, stream biologists have focussed on the algal (autotrophic) component of attached stone-surface communities (e.g., Nielsen 1950, McIntyre 1973), and although we agree with Minshall (1978) that the importance of autotrophic production should not underestimated, we believe that heterotrophic elements which are not restricted to well lit surfaces may play a major part in the transfer of energy to benthic invertebrate communities.

Table 2 Particle size distribution (percent dry weight) of fine particulate organic matter (< 1 mm diameter) present in sediment samples from 3 sites along Manson Creek, a beech forest stream in the Craigieburn Range, South I., Mar 1980. Shredders were absent from the first order tributary (Site a), but present (*Zelandopsyche ingens*) at Site b; extensive filamentous algae present at Site c. Shredders produce particles mainly in the size range marked *, whereas particles in guts of browsers are much smaller ("").

Particle size class (μm)	Sites a 1st order tributary in forest	b 3rd order stream in forest	c 3rd order stream in open
501–1000	22	28	72
251–500*	25	27	19
91–250	16	25	5
46–90**	15	8	2
< 46	22	12	1

The emphasis placed on shredder-feeding pathways by Cummins and co-workers (e.g., Cummins 1974, Petersen & Cummins 1974) has turned the attention of steam ecologists away from stone-surface communities, and even when the former are obvious we would still expect to find well developed organic layers supporting significant secondary production.

In fast-flowing natural streams, fungi and bacteria—the main living heterotrophs within the organic layer—obtain much of the carbon required for their growth and maintenance in dissolved form from the surrounding water (McDowell & Fisher 1976, Iversen & Madsen 1977, Geesey et al. 1978, Dahm 1981). Its exact source is unclear, but is assumed to include algal exudates and leaf leachates as well as dissolved materials in groundwater, throughfall, surface runoff, and other CPOM leachates (Lock & Hynes 1976, Dahm 1981). We contend that organic layers and associated FPOM are the main food sources of benthic invertebrates in fast-flowing New Zealand streams. About 85% of the non-carnivorous insects in South Island streams surveyed by Cowie (1980) and J. S. Rounick (unpubl. results) fed in this way, and detrital particles, rather than intact algal cells, predominated in gut contents of most species from both open and forested streams.

CPOM, when it occurs, may be important primarily as a source of dissolved organic matter utilised by microorganisms forming part of the organic layers which represent one of the most stable (Cowie 1980), and hence reliable, carbon sources in the lotic environment.

Finally, Vannote et al. (1980) have suggested that stream communities evolve to utilise energy inputs

with a high degree of efficiency and temporal uniformity, and according to Vannote & Sweeney (1980) they are highly structured entities. We see this as a contentious proposal, given the naturally heterogeneous and unpredictable nature of stream environments. Cummins's (1974) paper on stream ecosystem structure and function, although written from a limited data base, has been influential in popularising such a viewpoint—typified by Richardson's (1980) statements that "in woodland streams where leaf inputs are the chief plant materials available there is a strikingly complex set of species interactions", and "the species of each stage are clearly dependent on the species of all previous stages of leaf breakdown". As Richardson pointed out, animals and decomposers lend themselves to such organismic (i.e., community-as-organism) notions of the community, a view fostered by modern emphases on ecosystems, energy flow, and biotic influences on community structuring. Vannote & Sweeney (1980) and Vannote et al. (1980) apparently accepted this dogma when they suggested that stream communities have evolved to utilise energy inputs in a very efficient manner, a view implying (it seems to us) that natural selection operates at the community level!

On the face of it, stream ecosystems appear to be anything but integrated, closed systems displaying tight, or complex (cohesive) organisation, feedback loops, and so on. Rather, they are dominated by continual, but not necessarily predictable, recruitment of materials and organisms from outside (energy, nutrients, structural elements such as logs, invading insects) and losses or displacement of some of these downstream, and it is only the continual nature of their supply which serves to perpetuate stream communities. Physically controlled communities, especially those in unstable and unpredictable environments—as are New Zealand streams—are likely to be highly individualistic (as opposed to organismic) in nature, consisting of species geared towards colonising and saturating a physically demanding habitat, and not towards fine-tuned accommodation with co-existing species (Richardson 1980).

In addressing the problem of how to approach community-level phenomena in streams, Reice (1980) concluded that stream communities were very fluid and could best be interpreted as the transitory result of many individual population dynamics—a view with which we are in sympathy. Extending this to Vannote & Sweeney's (1980) contention that streams contain "highly structured communities" in a state of dynamic equilibrium (Vannote et al. 1980) must be considered a giant and tenuous step.

EPILOGUE

Let us return to the questions posed at the start of this paper. By now it should be clear that New Zealand streams do differ in a number of respects from those which have been intensively studied in North America and from which the river continuum concept has been developed. Why are they different? We suggest that to a large extent this is a function of the generally steep and youthful topography of New Zealand, the heavy and temporally unpredictable rainfall, and the nature of our upland catchments with their low timberlines, low biomass native forest, and paucity of deciduous trees. These features have resulted in New Zealand streams having poor retention characteristics and, consequently, biological communities centred around the direct utilisation of CPOM energy sources can rarely exist. In terms of the Cummins (1975) and Vannote et al. (1980) continuum models they are essentially decapitated systems, the equivalent, regardless of stream order, of Cummins's (1975) intermediate-sized rivers.

Finally, how realistic is the river continuum concept of Vannote et al. (1980) as a summary of river ecosystem structure and function as currently understood? Whereas in general it may be a fair description of those North American streams on which it is largely based, we would be surprised if some of the points and reservations raised above did not apply to them too. Clearly, considerably more work and data collection are required to test the concept adequately.

We predict that rivers arising high in the American Rockies and many other alpine regions will have ecosystem characteristics essentially like those in New Zealand, whereas those of ephemeral Australian waterways, English chalk streams, and the brown-water rivers of northern Canada are likely to be quite different and also poorly accommodated by the schemes of Vannote and his colleagues.

The river continuum concept, like so many generalisations, is bound to have numerous exceptions. The question then becomes: Are the exceptions so many as to invalidate the generality of the scheme? We are inclined to think so.

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CHAPTER VII

GENERAL DISCUSSION

I will approach this final section by reiterating the three questions asked in the General Introduction (Chapter I) and by discussing the answers yielded as a result of my research. I will then continue on to a general discussion of the topic of carbon pathways in streams.

1. *Why are shredders rare in New Zealand streams and what determines their sporadic occurrence?*

One explanation for the paucity of shredders in New Zealand put forward prior to my study was that for biogeographical reasons the fauna lacked groups which could feed in this way (Winterbourn, 1978d). It is true that shredders are poorly represented in New Zealand both in total numbers of species and in abundance of individuals within most streams (Winterbourn *et al.*, 1981, Chapter VI). Although zoogeographic reasons may at least partly explain the low numbers of species, they do not explain why those species which are present are not abundant. As demonstrated in Chapter V a core fauna of invertebrates is widely distributed in New Zealand streams of many forest types and some shredders are amongst them. These include species of Oeconesidae and the stonefly *Austroperla cyrene*.

Winterbourn (1978d) also suggested that the leaves of the predominant riparian trees in New Zealand, particularly beech (Fagaceae) with its thick cuticle, could be unpalatable to many aquatic insects and a further factor contributing to the lack of shredders. This now appears unlikely as it is well established that *Zelandopsyche ingens* feeds almost exclusively on beech leaves and wood (and larvae did so and grew when caged with beech litter in Craigieburn Cutting Stream, a stream lacking a natural population of shredders). Further, Winterbourn (1982) found that *Z. ingens* larvae can digest and assimilate the carbohydrate and lipid components of beech litter with the aid of gut bacteria indicating that leaves are not simply carriers of microbial food. *A. cyrene* has also been found to feed actively on a diet of mountain beech leaves and grow (M.J. Winterbourn, pers. comm.) and while not yet documented it is likely that other oeconesids feed on the leaves of broadleaf and podocarp species in various parts of the country (Chapter V). The microflora colonising leaves also is digested by New Zealand shredders as is the case elsewhere (Winterbourn & Davis, 1976). Oxygen consumption rates of leaves from several indigenous New Zealand trees and exotic species incubated in Middle Bush Stream fell within the range of values obtained

overseas for species which serve as food for shredders, suggesting that microbial "conditioning" of New Zealand natives is comparable to that elsewhere.

Organic matter retention is clearly the key factor controlling shredder distribution and abundance in New Zealand streams as demonstrated in Chapter II. Retention is closely related to stream bed stability and the presence of large stones or boulders or log jams which act as long-term retaining devices. As indicated by the stream surveys (Chapter V) and general observations (Winterbourn *et al.*, 1981) New Zealand streams overall are unstable, lack large wood debris and are flood prone, characteristics which together have mitigated against the development of large populations of shredders.

2. *If shredder populations are not abundant in New Zealand forest streams, and therefore are not operating as intermediaries in movement of carbon through food chains, then what are the major carbon pathways which support the large number of invertebrates in New Zealand streams?*

Using Winterbourn's (1976) suggestion that the organic layer on stones could be the main carbon source utilised by benthic invertebrates, work was carried out to document the formation, structure, existence and utilisation of the organic layers on stones.

Several authors have suggested that DOC plays an important role in aquatic food chains as a source of nutrients and energy incorporated by micro-organisms colonising particulate materials which, in turn, are ingested by filter and deposit feeders. Such pathways have been suggested for freshwater lentic (Paerl, 1978), lotic (Lock & Hynes, 1976; Mulholland, 1981b), estuarine (Gallager *et al.*, 1976; Newell, 1981) and marine (Parsons & Seki, 1970) ecosystems. However, despite these suggestions few, if any, studies have actually documented the transfer of DOC to POC and thence macroconsumers. I believe my work clearly demonstrates that stone surface organic layers are sites (as suspected by Lock & Hynes, 1976 and Winterbourn, 1976) of such transfer which may represent the major carbon pathway operating in many streams. Much work is still required on organic layer dynamics from several perspectives (e.g., biochemical, microbiological and at the micro-ecosystem level) in order to understand the interactions of the components within the layer itself.

Organic layers are almost certainly universal phenomena occurring in almost all streams though to date their treatment in the literature has been cursory (see Chapter III). Why have they received so little direct attention? First, as pointed out in Chapter III, what little emphasis there has been generally has been directed at their algal components rather than the heterotrophic ones. As most recent stream work has tended to play down the significance of algal production in small, temperate forest streams (see Minshall, 1978 for a discussion), the other components of the aufwuchs in streams from which general conceptual models have been drawn (e.g., Cummins, 1974; Boling *et al.*, 1975) have been largely ignored. Microbiologists have inadvertently pointed to the potential importance of heterotrophic elements of organic layers, a result of their interest in bacterial attachment (e.g., Gessey *et al.*, 1977; Costerton *et al.*, 1978; Gessey *et al.*, 1978) though the ecological implications of the organic layer, as outlined in Chapter II, have not been considered in their work.

The influence of entomologists on the development of stream ecosystem concepts has also been instrumental in focusing attention in particular ways. Many currently active ecologists entered the field as entomologists with an interest in aquatic insects, e.g., K.W. Cummins, N.H. Anderson and H.B.N. Hynes, and their attention was drawn to the most obvious, and to them the most interesting, series of interactions in streams; the shredder-microbial-detrital complex. Studies emphasising detrital carbon flow were in vogue at this time as a result of IBP work in terrestrial biomes, and must have influenced aquatic ecologists who have adapted terrestrial methods and concepts in studying decomposition in streams (Chapter II). The direction given by K.W. Cummins to much of this work has been considerable, particularly through his 1973 and 1974 papers. His functional feeding group approach (1973) and "peanut butter and cracker" analogy (1974) have become widely accepted and have been quoted by ecologists outside the field (e.g., Richardson, 1980) as being representative of current stream theory. A series of papers by Cummins and others (e.g., Petersen & Cummins, 1974; Anderson & Grafius, 1975; Boling *et al.*, 1975; Meehan *et al.*, 1977; Short & Maslin, 1977; Anderson & Cummins, 1979; Ward & Cummins, 1979; Vannote *et al.*, 1980; Hawkins & Sedell, 1981) are evidence of this approach. Another example of his influence is the over-interpretation of Ross (1963) discussed in Chapter V and its non-critical acceptance by subsequent workers.

I believe the search for other carbon pathways in stream ecosystems has been held in check over the last decade because of a too ready acceptance of the significance of shredder feeding and the emphasis placed on CPOM as a primary source of energy in streams. The New Zealand experience has pointed to the necessity for investigating alternative carbon pathways whose significance may well be considerable even where leaf inputs and shredders abound.

3. *What is the relative significance of allochthonous and autochthonous material as a source of energy utilised by benthic invertebrates in contrasting stream types?*

Stable carbon isotope analysis demonstrated that the same or closely related animal species apparently utilised allochthonous and autochthonous materials depending on their "availability" (e.g., as in open vs shaded streams and at forested compared with logged sites). Few animals appeared to be restricted to a particular site or type of stream because of food type. Additionally, the surveys of invertebrate distribution in relation to forest type (Chapter V) demonstrated that a common nucleus of taxa is present in all forest types, indicating an inherent flexibility or ecological generality of the fauna. Additionally, I demonstrated that larvae of *Deleatidium*, which are abundant in New Zealand streams, appear to be utilising autochthonous carbon even when it is apparently in "short" supply in a stream which should be "heterotrophic" and "allochthonous based". While a number of measurements of allochthonous and autochthonous inputs to stream ecosystems have been made (e.g., Fisher & Likens, 1973; Fisher, 1977; Mulholland, 1981a; see Minshall, 1978 for a compilation of these values), the degree of transfer of these inputs to animal communities has been largely a matter of speculation prior to this work. With tools like stable carbon isotope analysis available, greater clarification of trophic relationships within streams can be expected in the future.

General Overview

Carbon budgets have demonstrated that forested stream ecosystems process only a small percentage of the total energy entering them. For example, Bear Brook, New Hampshire had an ecosystem efficiency (respiration/total input) of 34% (Fisher & Likens, 1972), Middle Bush Stream, Canterbury, New Zealand 16% (McCammon, 1978) and Fisher (1977)

found that over 96% of the organic matter entering and leaving a segment of the Fort River, Massachusetts did so in transport. When carbon processing by the macrobenthos is considered, the percentage utilised is seen to be extremely small. Fisher & Likens (1973) calculated that macroconsumer respiration accounted for approximately 1% of energy loss from Bear Brook and similarly McCammon (1978) estimated that macroconsumers utilised less than 1% of the total inputs to Middle Bush Stream. These coarse, mass-balance approaches to carbon budgeting in streams deal with whole ecosystem processes and provide limited information on intra-system transfer of carbon particularly with respect to macroconsumers. Also, such estimates are of questionable accuracy because in most cases respiration has been estimated indirectly by difference (e.g., Fisher & Likens, 1973; McCammon, 1978). This assumes that streams are in an annual steady state with respect to organic matter storage. This is a highly debatable point given the variability in organic matter losses or gains in high or low discharge years.

If animal-oriented ecologists are to better understand consumer processing of carbon then more emphasis must be placed on those organic carbon inputs which funnel up to consumers themselves, even if they represent less than 1% of the total input to the ecosystem. For example, if the organic layer on stone surfaces is an important site of carbon transfer to the benthos, then more attention should be directed to the role of DOM inputs and their utilisation by the layer as has been done by Dahm (1981). Future investigations into the abilities of both micro- and macroconsumers to utilise a variety of potential sources of carbon (e.g., specific components of DOM, structural plant materials, plant proteins, fungal and bacterial polysaccharides) should prove useful in increasing our understanding of these processes. Substrate uptake experiments using radioactively labelled components of DOM as well as invertebrate gut enzyme work in the vein of Martin *et al.* (1980) and Winterbourn (1982) can yield valuable information on consumer processing abilities. In turn, the results of such studies can direct the researcher's attention to particular components of a mass-balance budget and so provide necessary integration of the mass-balance and intra-system approaches.

In New Zealand, many stream ecosystems appear to be strongly dominated by physical factors. The physical structure of the stream bed and the hydrological regime dictate the framework within which the biological community functions. Physical factors affect quantities of

allochthonous material entering and leaving a stream reach (McCammon, 1978), regulate autochthonous inputs by influencing light levels as a result of valley configuration and by variations in the flow regime (Rounick & Gregory, 1981). Flow patterns can also affect invertebrate distribution and abundance (Winterbourn, 1976; Cowie, 1980). Generally, biotic interactions such as competition (both intra- and interspecific) and predation appear to be important only at the local level (see Peckarsky & Dodson, 1980; Hart, 1980). In essence then, I see stream ecosystems as physically and climatically dominated entities whose dynamics are most easily understood when viewed in this light.

In order to gain a fuller understanding of carbon pathways in streams, the mass-balance approach needs to be integrated with studies of intra-system processes within the context of the overriding physical environment.

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APPENDIX I. Total numbers of invertebrates present in three surface and buried incubated leaf bags removed from Middle Bush Stream and Craigieburn Cutting Stream on each of eight sampling dates. Numbers in parentheses are for buried bags. * - denotes presence but not enumerated.

	Middle Bush Stream								Craigieburn Cutting Stream							
Weeks:	2	4	6	8	10	12	16	22	2	4	6	8	10	12	16	22
Turbellaria																
Neppia montana (Nurse)	2(0)	2(0)	1(0)	1(0)	2(0)	4(0)	0(0)	1(0)	0(0)	0(0)	3(0)	1(0)	2(2)	2(1)	2(1)	1(0)
Oligochaeta																
Eiseniella tetraedra (Savigny)	0(0)	1(2)	1(1)	2(0)	2(2)	1(0)	3(4)	0(1)	0(0)	0(0)	0(0)	2(0)	0(0)	0(2)	1(1)	1(0)
Nematomorpha																
Gordius sp.	0(0)	0(2)	1(1)	2(2)	1(1)	4(1)	2(1)	0(2)	1(0)	2(1)	2(2)	1(0)	2(1)	1(1)	2(0)	3(2)
Insecta																
Ephemeroptera																
Deleatidium sp.	1(0)	14(0)	17(6)	13(8)	19(8)	26(11)	20(8)	15(11)	2(3)	1(3)	4(5)	7(3)	8(2)	4(2)	6(4)	3(1)
Nesameletus sp.	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	1(3)	1(0)	2(4)	2(1)	4(3)	8(2)	3(2)	5(1)
Trichoptera																
Olinga feredayi (McLachlan)	2(0)	0(0)	1(0)	4(0)	2(0)	1(0)	0(2)	1(2)	1(0)	3(3)	2(0)	1(1)	0(0)	2(0)	1(2)	4(0)
Philorheithrus agilis (Hudson)	3(4)	1(6)	7(7)	3(1)	1(3)	0(4)	5(5)	2(1)	0(0)	1(1)	1(1)	1(1)	3(2)	2(1)	4(0)	1(2)
Ryacophilidae	0(0)	1(0)	1(0)	2(3)	0(2)	1(1)	1(2)	1(1)	0(1)	0(1)	2(1)	1(1)	0(1)	1(2)	1(1)	2(1)
Zelandopsyche ingens Tillyard	6(0)	14(4)	27(8)	29(0)	30(0)	38(5)	6(2)	0(20)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Plecoptera																
Austroperla cyrene (Newman)	0(1)	3(0)	6(2)	5(1)	3(0)	2(2)	4(1)	0(0)	0(1)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Spaniocerca zelandica Tillyard	3(3)	9(2)	11(4)	8(0)	14(6)	11(0)	6(7)	1(5)	0(0)	1(1)	0(0)	1(0)	0(2)	0(0)	0(0)	0(0)
Stenoperla prasina (Newman)	2(0)	2(0)	0(0)	2(0)	0(0)	1(0)	3(0)	1(0)	0(0)	0(0)	0(0)	0(0)	1(0)	0(0)	1(0)	1(0)
Zelandobius sp.	0(0)	3(1)	5(0)	6(3)	5(0)	4(2)	7(0)	0(0)	0(0)	0(0)	1(0)	0(0)	0(0)	1(1)	0(0)	0(1)
Diptera																
Chironomidae	*(*)	*(*)	*(*)	*(*)	*(*)	*(*)	*(*)	*(*)	*(*)	*(*)	*(*)	*(*)	*(*)	*(*)	*(*)	*(*)
Tipulidae	0(0)	0(0)	0(1)	1(0)	0(2)	1(0)	0(1)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(1)	1(0)	0(0)
Coleoptera																
Elmidae	0(0)	1(0)	0(2)	1(0)	2(0)	0(0)	1(2)	0(0)	0(1)	0(1)	1(0)	1(1)	0(0)	0(0)	1(1)	2(2)
Helodid Species A	0(0)	1(1)	0(1)	3(1)	0(1)	1(1)	3(2)	1(0)	0(0)	0(0)	0(0)	1(0)	0(0)	0(1)	0(0)	0(0)
Helodid Species B	1(0)	0(0)	1(0)	1(1)	0(0)	2(0)	0(3)	2(2)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Hydraenidae	1(1)	1(1)	0(0)	1(2)	0(0)	0(3)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	1(0)
Staplylinidae	0(0)	0(0)	1(1)	0(0)	1(0)	1(0)	0(0)	0(0)	0(0)	0(0)	0(0)	1(0)	3(0)	1(0)	0(0)	0(0)

Appendix IIa Location, date sampled, forest type, physical and faunal characteristics of 43 sites for work in Chapter V.

Study Site	NZMS Grid Reference	Date Sampled	Forest Type[1]	Width (m)	Gradient (°)	Stability Rating[2]	No. of taxa	Top-5 fauna[3] (% abundance)	Shredder Abundance Rating[4]
NORTH ISLAND									
Jerry St. (Trib.)	N44 101450	1/ 2/80	PH	0.5	8	101	11	C(53), A(22), M(9), AA(6), FF(3)	2
Kahutawara (Trib. #1)	N149 115233	23/ 1/80	PH	1.5	10	98	6	GG(51), A(27), C(5), FF(5), EE(5)	2
Kahutawara (Trib. #2)	N149 106210	23/ 1/80	PH	0.8	2	60	6	II(46), D(15), A(15), C(8), M(8)	3
Kirikiri Stream (Trib.)	N49 086215	31/ 1/80	PH	0.5	12	139	1	A(100)	1
Mahakirau River (Trib. #1)	N44 057608	1/ 2/80	PH	0.3	15	122	3	A(50), FF(25), HH(25)	1
Mahakirau River (Trib. #2)	N44 055606	1/ 2/80	PH	0.6	9	114	6	C(33), A(25), M(17), FF(8), H(8)	2
Mangamate Stream	N112 250811	13/ 2/80	PHB	1.0	5	97	12	O(24), A(22), Y(13), L(9), M(9)	3
Mangawhero Stream (Trib.)	N121 996597	13/ 2/80	PHB	4.0	15	72	18	A(29), Y(15), DD(10), J(8), H(7)	2
Ohau Stream (Trib.)	N152 890986	14/ 2/80	PH	2.3	9	88	6	C(64), A(25), M(7), E(2), Y(1)	1
Patea River	N119 803584	17/ 2/80	PH	5.0	0.7	79	20	Q(31), A(25), C(15), K(9), CC(4)	1
Retaruke River (Trib.)	N121 852682	13/ 2/80	PHB	0.7	0.5	72	6	L(32), X(21), Y(21), A(16), E(10)	3
Sparrow Stream	N44 068603	1/ 2/80	PH	1.8	8	147	4	A(43), P(29), O(14), N(14)	1
Taruru Creek	N49 035305	31/ 1/80	PH	0.8	10	100	8	C(37), A(33), B(12), M(6), F(4)	1
Tiritea Stream	N149 163257	22/ 1/80	PH	5	3	99	10	A(33), K(19), GG(11), C(8), E(8)	3
Tiritea Stream (Trib. #1)	N149 166254	22/ 1/80	PH	1	8	70	16	A(36), C(22), M(6), E(4), Y(4)	3
Tiritea Stream (Trib. #2)	N149 163249	22/ 1/80	PH	1	6	87	10	C(29), M(29), A(14), Y(9), B(9)	2
Te Popo Stream	N119 715611	17/ 2/82	PH	3.5	4	77	30	A(24), Y(20), J(12), I(6), F(5)	3

Cont'd

The Wash	N76 762010	12/ 2/80	P	0.5	1	122	6	A(45), Y(20), GG(15), C(10), B(5)	1
Whalebone Creek	N44 010426	31/ 1/80	PH	2.2	4	99	7	C(43), A(19), B(12), K(12), GG(7)	1
SOUTH ISLAND									
Ackland Creek	S91 790138	22/11/81	B	1.3	4	92	12	A(45), E(12), DD(10), AA(9), J(7)	2
Andrews Stream (Trib.)	S59 265221	16/ 3/80	B	2.5	6	68	6	L(33), C(29), K(19), U (10), A(5)	1
Blue Duck Creek	S49 048069	15/ 5/81	PH	4.5	1.5	90	27	A(40), N(15), Q(10), P(8), T(4)	1
Boakes Creek	S46 813863	21/ 5/81	B	1.5	15	80	10	A(71), EE(10), E(4), K(4), F(4)	1
Craigieburn Cutting Stream	S66 216030	15/ 3/80	B	2.0	11	128	16	A(60), B(22), G(4), Y(2), DD(2)	1
Dog Stream	S54 207795	19/12/79	P	3.0	2	97	8	A(48), N(18), K(13), P(8), E(5)	1
Forest Park Stream	S66 200034	10/ 4/80	B	1.3	15	93	11	G(22), B(18), K(16), A(15), L(9)	3
Glentui River	S67 180954	17/12/81	B	5	1.5	69	14	A(54), K(11), W(10), J(7), C(4)	2
Kaituna River	S84 095334	1/ 5/76	PH	4.5	5.3	84	32	C(27), N(20), A(20), K(14), GG(4)	3
Manson Creek	S66 225065	15/ 3/80	B	3.5	11	70	19	A(44), B(25), F(9), Y(4), R(3)	3
Manson Creek (Trib.)	S66 225056	15/ 3/80	B	1.5	15	134	5	A(63), B(31), F(2), O(2), P(2)	1
Middle Bush Stream	S66 236173	15/ 3/80	B	1.0	23	90	14	L(31), G(29), R(12), A(11), EE(7)	3
Mikonui Stream	S59 798760	16/ 5/81	PH	1.5	3.7	76	19	A(25), N(14), E(13), L(9), G(8)	3
Nature Walk Creek	S54 213798	19/12/79	B	4	8	75	7	A(59), K(22), GG(9), C(4), L(2)	3
Otira Creek	S59 056436	23/ 5/81	B	2.5	15	110	15	A(23), G(23), J(8), BB(8), E(5)	1
Palmer Creek	S49 922008	15/ 5/81	PH	3.5	23	60	16	F(34), A(34), N(10), K(3), CC(3)	2

Cont'd

Paterson Creek	S46 814894	21/ 5/81	B	3	10	107	10	A(81), F(6), J(4), E(3), S(2)	1
Powerline Gully	S38 256336	20/ 5/81	PHB	3.5	2	98	7	A(44), C(26), L(12), GG(9), G(3)	3
Rata Stream	S91 765133	23/11/81	B	8	12	127	5	A(90), B(4), DD(2), E(2), F(2)	1
Rough Creek	S46 700962	21/ 5/81	B	3	6	78	8	A(81), Y(4), E(4), F(4), J(4)	2
Tasman Smith Reserve Stream	S110 412591	15/ 1/82	PH	2	4	83	10	A(27), F(20), C(18), GG(9), K(7)	2
Trotters Creek	S146 295381	19/ 4/81	PH	5.5	0.4	99	20	A(26), Y(21), V(11), K(9), N(8)	2
Waterfall Creek	S54 212798	18/12/79	B	4.5	4	66	10	A(29), K(26), H(14), L(7), GG(6)	3
Belltopper Falls Stream	N.A.	11/11/81	PH	3	0.5	41	9	II(49), O(26), FF(6), Z(6)	3

[1] B - Beech
PHB - Podocarp-hardwood-beech
PH - Podocarp-hardwood
P - Pine plantation

[2] from Pfankuch (1975)

[3] See Appendix IIb for key to invertebrate taxa

[4] Shredder abundance rating: 1 - absent
2 - present - 0.1 to 3.0% of total fauna numbers
3 - abundant - >3.0% of total fauna numbers

Appendix IIb Key to invertebrate fauna listings presented in Appendix IIa.

Member of Top-5	Code
Ephemeroptera	
Deleatidium	A
Nesameletus	B
Coloburiscus humeralis	C
Arachnocolus phillipsi	D
Plecoptera	
Stenoperla prasina	E
Zelandoperla	F
Spaniocerca zelandica	G
Austroperla cyrene	H
Megaleptoperla grandis	I
Zelandobius	J
Trichoptera	
Olinga feredayi	K
Oeconesidae	L
Orthopsyche	M
Aoteapsyche	N
Hydrobiosella	O
Hydrobiosis	P
Helicopsyche	Q
Philorheithrus agilis	R
Costachorema	S
Polyplectropus	T
Psilochorema	U
Pycnocentria	V
Pycnocentrodes	W
Triplectides obsoleta	X
Coleoptera	
Elmidae	Y
Helodidae	Z
Ptilodactylidae	AA
Diptera	
Austrosimulium	BB
Aphrophila neozelandica	CC
Other Tipulidae	DD
Oligochaeta	
Eiseniella tetraedra	EE
Decapoda	
Paranephrops	FF

Cont'd

Appendix IIb - Cont'd

Megaloptera	
Archichauliodes diversus	GG
Gastropoda	
Potamopyrgus antipodarum	HH
Amphipoda	II